UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ACTIVITÉ, EXPLORATION ET LEUR RELATION AVEC L'UTILISATION DE L'ESPACE PAR LES INDIVIDUS DANS UNE POPULATION SAUVAGE DE TAMIAS RAYÉS (*TAMIAS STRIATUS*)

MÉMOIRE

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PAR

PIERRE-OLIVIER MONTIGLIO

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AVANT PROPOS

Je présente ce mémoire sous la forme de deux articles. Le premier article, intitulé « Individual variation in temporal activity patterns and the measurement of activity/exploration in an open-field test in the eastern chipmunk (*Tamias striatus*)» est une note méthodologique sur l'analyse du test d'arène pour quantifier le niveau d'activité/exploration des animaux. Les auteurs seront Pierre-Olivier Montiglio, Dany Garant, Don Thomas, et Denis Réale. POM a conduit les tests, a fait les analyses et a rédigé l'article. À toutes ces étapes, il a été encadré par DG et DR, qui ont également fournis leur support au financement et à la logistique du travail de terrain. DT a participé à l'administration et à la logistique du projet de recherche à long terme sur le tamia rayé dans lequel cette étude s'inscrit. Le deuxième article, « Activity/exploration during open-field tests, space use and mate search in the eastern chipmunk (*Tamias striatus*) », est une étude reliant le niveau d'activité et d'exploration des mâles à leur comportement de recherche de partenaires sexuels, estimé par leur patron d'utilisation de l'espace. Les auteurs sont Pierre-Olivier Montiglio, Denis Réale et Dany Garant. POM a participé à la saisie des données, a fait les analyses, et a rédigé l'article. DR et DG ont tout deux participé à chacune des étapes par leur encadrement et leur supervision.

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TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ GÉNÉRAL

L'approche du comportement basée sur les coûts et les bénéfices montre que les systèmes polygynes peuvent favoriser une plus grande mobilité des mâles et des comportements de recherche de partenaires sexuels. Ce mémoire est une étude écologique tentant de préciser le lien entre la personnalité des individus et leur comportement de reproduction. Pour ce faire, nous avons étudié une population de tamias rayés (*Tamias striatus*) au Québec. Chez le tamia rayé, les mâles font des rondes d'inspection pour maximiser leurs chances de féconder les femelles. Il est très probable que les mâles soient face à un compromis entre le nombre de femelles visitées et l'effort investi sur chacune d'elle. Nous avons mesuré la personnalité des individus par des tests d'arène, mesurant le comportement des individus dans un environnement nouveau. Pendant ces tests, les individus peuvent montrer des patrons temporels d'activité et d'exploration différents. Si les individus montrent des patrons temporels différents, le score global d'activité et d'exploration des individus est susceptible d'être biaisé par la durée du test. Notre premier objectif est de montrer comment, en utilisant des modèles généralisés mixtes, il est possible de prendre en compte des différences de patron temporel durant les tests d'arènes. Nous avons utilisé des modèles généralisés mixtes analysant le temps passé actif durant les tests d'arènes afin de prendre en compte des facteurs environnementaux et d'estimer la constance du niveau global et du patron temporel d'activité et d'exploration des tamias dans l'arène. Les individus ont montré des patrons temporels d'activité et d'exploration différents, suggérant un gradient de proactivité dans la population. Nos estimations de reproductibilité sont similaires à celles rapportées par d'autres études. Nos résultats montrent que les études utilisant le test d'arène devraient prendre en compte le patron temporel de la réponse des individus, pour permettre une meilleure compréhension des traits de personnalité. Dans le second chapitre, nous déterminons comment les différences d'activité et d'exploration entre les tamias mâles affectent leur utilisation de l'espace pendant la reproduction (reflétant le comportement de recherche de partenaires sexuels). Nos objectifs sont (1) de comparer les patrons d'utilisation de l'espace par les mâles et les femelles pendant la reproduction et en absence de reproduction, et (2) de déterminer si l'espace supplémentaire utilisé par les mâles pendant la reproduction est relié à leur niveau d'activité et d'exploration. Nous avons réalisé des sessions de capture durant deux étés consécutifs (un été comportant une saison de reproduction et un été sans reproduction). Nous avons calculé le domaine vital et un indice de la surface visitée exceptionnellement par les mâles par la méthode des polygones minimums convexes. Nos résultats montrent que les mâles ont utilisé une surface plus importante durant l'année avec reproduction comparée à l'année sans reproduction estivale. Les femelles n'ont pas montré de différences entre les deux années. La surface utilisée par les individus était limitée par la proportion de mâles avoisinants. L'activité et l'exploration étaient reliés différemment à la surface utilisée selon les années. La surface visitée exceptionnellement n'était pas affectée par le niveau d'activité et d'exploration. Pour les femelles, cette surface était plus importante en absence de reproduction, suggérant ainsi qu'elles limitent leurs déplacements durant la gestation et l'allaitement. La personnalité peut affecter des aspects de la reproduction, ceci devrait faire l'objet d'études plus approfondies.

Mot clés : Personnalité, Reproduction, Tamias striatus, Activité.

INTRODUCTION GÉNÉRALE

I.1 Les deux postulats de l'écologie comportementale

L'écologie comportementale tente de comprendre comment le comportement résulte à la fois de l'histoire évolutive des espèces et des populations, ainsi que des caractéristiques des individus et des conditions environnementales prévalant durant leur développement (Danchin, Giraldeau et Cézilly, 2005). Ainsi définie, l'écologie comportementale analyse le comportement animal dans une perspective évolutive. Comme la plupart des disciplines évolutives, elle considère ainsi que la sélection tend à optimiser les structures biologiques et les traits d'un organisme (Krebs et Kacelnik, 1991). À partir de ce premier postulat, on considère donc que, par leur comportement, les organismes maximisent leur aptitude phénotypique (Danchin, Giraldeau et Cézilly, 2005).

Si la sélection à long terme tend à optimiser les traits exprimés par un organisme, alors l'analyse de la fonction de ces traits nous permet de comprendre comment la sélection naturelle a agit sur ces derniers. Par exemple, la morphologie des membres d'un animal peut être comprise par la connaissance des lois physiques et des forces mécaniques qui sont exercées sur celui-ci (Danchin, Giraldeau et Cézilly, 2005). De la même manière, l'écologie comportementale suppose que, face à une situation particulière, les individus peuvent utiliser des tactiques alternatives. On suppose que chacune de ces alternatives est associée à des coûts et des bénéfices différents en terme de reproduction et de survie et que les individus expriment l'alternative possédant le ratio entre les bénéfices et les coûts le plus important (Krebs et Kacelnik, 1991). Cette approche possède l'avantage de permettre de prédire quel comportement l'organisme exprimera dans une situation donnée.

L'approche classique en écologie comportementale se distingue cependant d'autres disciplines évolutives par le fait que les recherches qui la constituent se limitent pour la plupart au phénotype des individus. Cette simplification provient d'un second postulat qui

considère que le système génétique à la base d'un comportement peut être traité comme s'il était le plus simple possible (Grafen, 1991). Selon le raisonnement sous-jacent, puisqu'un trait phénotypique résulte d'un grand nombre d'interactions, impliquant plusieurs loci, on peut modéliser l'ensemble de ces interactions par un système simple, caractérisé par un seul locus, et autant d'allèles qu'il y a de possibilités de phénotypes. Ainsi, lorsqu'on étudie un comportement donné, nous nous représentons le système génétique sous-jacent à ce comportement par un locus haploïde au niveau duquel chaque alternative serait représentée par un allèle différent. Les bénéfices reliés à chacune des stratégies peuvent être exprimés en termes de succès reproducteur, et la sélection devrait favoriser les allèles (ou alternatives) qui sont associées au succès reproducteur le plus important. Bien que certains traits ne se prêtent pas à une telle simplification, on considère qu'ils sont rares (Grafen, 1991). De plus, cette simplification convient très bien aux traits comportementaux, puisque ceux-ci ont tendance à être contrôlés par un très grand nombre de gènes et que leur expression peut être adéquatement modélisée comme un système comportant un locus haploïde possédant plusieurs allèles (Grafen, 1991). Cette approche possède l'avantage de permettre une étude du comportement au niveau phénotypique uniquement, sans se soucier des considérations génétiques sous-jacentes, qui sont souvent compliquées (voir Hadfield *et al.*, 2007 pour un exemple des limitations de cette approche).

I.2 Le comportement de reproduction

L'approche du comportement basée sur les coûts et les bénéfices adoptée en écologie comportementale a généré des contributions théoriques importantes dans l'étude du comportement de reproduction (Emlen et Oring, 1977; Trivers, 1972). Ainsi, on considère maintenant les systèmes de reproduction, non plus comme des attributs fixes des espèces, mais plutôt comme le résultat des stratégies de reproduction exprimées par les individus pour maximiser leur succès reproducteur (Clutton-Brock, 1989).

Les mâles et les femelles adoptent des stratégies de reproduction différentes. Cette divergence provient du fait que les femelles produisent un nombre limité de gamètes de

grande taille tandis que les mâles produisent des gamètes de petite taille en grande quantité (Bateman, 1948). Le succès reproducteur des femelles devrait donc être limité par les ressources qu'elles peuvent investir dans leur progéniture. Ainsi, les femelles tentent d'optimiser les ressources allouées à leurs jeunes et la qualité de leurs partenaires sexuels. À l'inverse, le succès reproducteur des mâles devrait être limité principalement par le nombre de partenaires auxquels ils peuvent accéder. Pour maximiser leur succès reproducteur, les mâles devraient donc plutôt maximiser l'accès et la fécondation de partenaires sexuels (Emlen et Oring, 1977; Trivers, 1972).

De ces différences de production des gamètes, il découle que les femelles sont, dans la grande majorité des cas, le sexe « limitant » et que la compétition pour les partenaires sexuels est plus importante entre les mâles qu'entre les femelles (Bateman, 1948). Les caractéristiques des femelles, telles que leur capacité à élever les jeunes seules ou non, la distribution des femelles réceptives dans le temps et dans l'espace, et l'étendue de leur domaine vital sont ainsi les principales sources de variation entre les systèmes de reproduction des mammifères (Clutton-Brock, 1989). Si le taux de reproduction des femelles peut être amélioré par la participation du mâle à l'élevage des jeunes, le système de reproduction social sera principalement un système de monogamie (pouvant néanmoins inclure des copulations hors couple, impliquant que certains mâles se reproduisent avec plus d'une femelle). Dans le cas contraire, le système de reproduction observé sera le plus souvent un système de polygynie où les mâles ne prodiguent aucun soin parental et tentent de copuler avec le maximum de femelles (Clutton-Brock, 1989). Le type de polygynie observé dépend ensuite de la plus ou moins grande capacité des mâles à défendre l'accès aux femelles réceptives (Emlen et Oring, 1977; Reynolds, 1996), qui dépend à son tour de la distribution des femelles fécondes dans l'espace et le temps.

Un mâle peut défendre l'accès à une femelle contre les autres mâles, si les femelles sont regroupées dans l'espace ou sont réceptives de manière asynchrone dans le temps (Clutton-Brock, 1989). Ainsi, chez certaines espèces d'ongulés, les mâles défendent plusieurs femelles, regroupées en harem (par exemple chez le cerf rouge, *Cervus elaphus*, Bonenfant *et al.*, 2004), ou encore ils défendent des territoires possédant une ressource nécessaire aux

femelles comme un point d'eau ou de nourriture (par exemple chez le Topi, *Damaliscus lunatus*, Gosling, 1991). Ces systèmes de reproduction, où les mâles sont en compétition directe pour les femelles, favorisent des traits qui confèrent un avantage dans les combats contre les autres mâles tels que des armes développées (par exemple les cornes, ou les crocs), la masse corporelle et l'agressivité (Preston *et al.*, 2003).

Si, à l'inverse, les femelles sont dispersées sur une grande surface, ou si leur reproduction est synchrone, un mâle donné pourra difficilement monopoliser l'accès aux femelles fécondes, et le système de reproduction sera le plus fréquemment un système de polygynie ou de promiscuité « de mêlée » (*scramble polygyny* ou *scramble promiscuity* en anglais) où les mâles ne prodiguent aucun soin parental, et tentent de copuler avec le maximum de femelles (Emlen et Oring, 1977). On considère que la polygynie désigne un système où les mâles copulent avec le même groupe de femelles durant une saison de reproduction, tandis que la promiscuité désigne un système où les mâles copulent avec n'importe quelle femelle réceptive (Clutton-Brock 1989). Ces deux systèmes impliquent également que plusieurs mâles copulent avec la même femelle et une compétition spermatique entre les mâles est possible (Birkhead et Hunter, 1990). La compétition spermatique peut favoriser l'évolution de plusieurs traits permettant aux mâles de maximiser leurs chances de féconder une femelle avec laquelle ils ont copulée (pour une synthèse, voir Birkhead et Hunter, 1990). Ainsi, chez certaines espèces, le sperme d'un mâle forme un bouchon copulatoire qui empêche le sperme des autres mâles de féconder la femelle. De tels bouchons sont observés par exemple chez les écureuils arboricoles (Koprowski, 1992) où une femelle donnée peut copuler avec un grand nombre de mâles durant sa période d'œstrus. La compétition spermatique peut également influencer la morphologie même des organes reproducteurs. Par exemple, le pénis de plusieurs espèces de libellules (*Argiae* sp.) possède des écailles orientées de manière à déplacer le sperme des autres mâles, augmentant ainsi les chances d'un mâle de féconder la femelle (Waage, 1986). Ces systèmes peuvent également favoriser certaines tactiques comportementales des mâles comme le fait pour un mâle de féconder une femelle puis d'en garder l'accès, tentant ainsi d'interrompre les copulations suivantes avec les autres mâles (Clutton-Brock, 1989).

Dans les cas où la compétition spermatique est limitée, les mâles qui trouvent les femelles plus efficacement ont un avantage en terme de succès reproducteur. Les traits ou les comportements permettant une détection plus efficace des femelles seront alors associés à un succès reproducteur plus important (Schwagmeyer et Woontner, 1986). Ces traits peuvent être des traits sensoriels. Par exemple, chez certaines espèces d'arthropodes, les antennes permettent aux mâles de détecter les femelles durant la reproduction, et les mâles qui possèdent des antennes plus longues détectent plus rapidement les phéromones ou les chants des femelles (Bertin et Cézilly, 2003a, b; Hanks, Millar et Paine, 1996). La compétition indirecte entre les mâles peut également favoriser des traits morphologiques impliqués dans la locomotion, qui permettront aux mâles de se déplacer rapidement jusqu'à la femelle ou de la suivre dans la mêlée (Able, 1999; Partridge, Ewing et Chandler, 1987; Partridge et Farquhar, 1983; Partridge, Hoffmann et Jones, 1987). De tels systèmes de reproduction peuvent également favoriser des traits cognitifs ou comportementaux, comme une habilité et une mémoire spatiales plus développées chez les mâles (Gaulin et Fitzgerald, 1986; Gaulin et Fitzgerald, 1989; Gaulin, FitzGerald et Wartell, 1990; Spritzer, Solomon et Meikle, 2005) ou une plus grande mobilité des mâles (Kappeler, 1997; Schwagmeyer, Parker et Mock, 1998).

Les mâles d'une même population peuvent également maximiser l'accès aux partenaires sexuels en utilisant différentes tactiques. Une tactique de reproduction peut se définir comme un assemblage de traits, pouvant regrouper des traits morphologiques, comportementaux ou physiologiques; et permettant aux mâles (par exemple) de féconder les femelles (Brockmann, 2001; Gross, 1996). Une tactique peut être déterminée génétiquement, ou tout simplement être constituée par le comportement qu'un individu donné adopte pour maximiser sa reproduction (Gross, 1996). La présence de tactiques alternatives peut être reliée à trois grandes explications. Elles peuvent être expliquées par le fait que les coûts et les bénéfices d'une alternative donnée sont différents d'un mâle à l'autre et donc que la tactique optimale est différente selon les mâles (on parle de tactiques dépendantes de la condition des mâles). Pour que des tactiques alternatives soient présentes il ne faut donc pas forcément qu'elles soient reliées à des aptitudes phénotypiques similaires, mais uniquement que l'alternative optimale soit différente selon les individus. Par exemple, chez *Dendrobias mandibularis*, une espèce de cafard vivant dans un climat désertique, les mâles qui possèdent des mandibules de

grande taille se reproduisent en défendant des territoires sur lesquels les femelles viennent se nourrir. À l'inverse, les mâles possédant de petites mandibules (incapables de défendre un territoire) copulent avec les femelles sur le feuillage et les fruits, loin des territoires défendus par les mâles dominants (Oliviera, Taborsky et Brockmann, 2008). Le choix de l'une ou l'autre de ces tactiques est associé aux caractéristiques corporelles du mâle, la taille des mandibules, qui influence sa capacité à combattre les autres mâles. Alternativement, les bénéfices et les coûts d'une alternative peuvent varier en fonction de la fréquence des tactiques dans la population. On s'attend alors à ce que ces tactiques soient maintenues à l'équilibre sous certaines proportions par une sélection dépendant de la fréquence (Maynard Smith, 1982). De telles tactiques, si elles sont à l'équilibre, devraient être associées à des succès reproducteurs équivalents. Les mâles de l'espèce *Paracerceis sculpta* (un isopode marin) constituent un exemple classique de ce type de stratégies. Les mâles de cette espèce peuvent se répartir en trois morphes distincts : les mâles α sont larges et défendent des harems de femelles, les mâles β ont une morphologie similaire aux femelles, tandis que les mâles γ sont de petite taille et s'infiltrent dans les harems à l'insu des mâles α. Ces trois types de mâles ont un succès reproducteur égal lorsqu'on les isole en présence de femelles. Cependant, lorsque ces trois morphes sont simultanément en présence de femelles, le succès reproducteur d'un type de mâle dépend de la fréquence des autres types dans la population. En nature, les trois tactiques ont un succès moyen équivalent (Shuster et Wade, 1991; 2003).

Les mâles peuvent également adopter des tactiques alternatives pour se reproduire dans les systèmes de reproduction polygynes ou de promiscuité. Par exemple, chez le tamia rayé (*Tamias striatus*), les femelles sont dispersées dans l'environnement (Elliott, 1978), et donc les mâles peuvent difficilement défendre l'accès aux femelles. Durant la saison de reproduction, les mâles font donc des rondes d'inspection pour visiter les femelles, afin de déterminer leur réceptivité et possiblement acquérir des informations sur leur territoire. Le jour de l'œstrus de la femelle, plusieurs mâles se réunissent sur son territoire et tentent activement de copuler avec elle (Elliott, 1978). Pour maximiser sa reproduction, un mâle pourrait diviser son effort de reproduction sur un nombre donné de femelles, dans la mesure où le nombre de femelles visitées se traduit par une réduction de l'effort consacré à chacune

des femelles. Le nombre de femelles visitées pourrait donc être influencé par le niveau d'activité et d'exploration des mâles.

I.3 Optimalité et limites à la plasticité phénotypique : personnalité et profil comportemental des individus

Comme l'illustre l'étude des systèmes de reproduction, l'écologie comportementale est axée sur la plasticité comportementale des animaux. On considère qu'un animal possède la capacité de modifier presque infiniment son niveau d'activité et d'exploration selon le risque de prédation (Hall, Humphries et Kramer, 2007; Houston, McNamara et Hutchinson, 1993; Sih, Kats et Maurer, 2003), ou selon le niveau de prédictibilité de l'environnement. Mais comme les individus ne peuvent pas ajuster parfaitement leur niveau d'activité et d'exploration aux conditions environnementales, des différences individuelles d'activité et d'exploration constantes dans le temps et d'une situation à l'autre sont toujours visibles entre les individus (Gosling, 2001; Réale *et al.*, 2007; Sih, Bell et Johnson, 2004; Sih *et al.*, 2004). Ces différences de comportement constituent la base des traits de personnalité (Carere *et al.*, 2005; Réale *et al.*, 2007). Les traits de personnalité, en particulier l'activité et l'exploration des individus, attirent de plus en plus l'intérêt des écologistes comportementaux. Un des objectifs prioritaires des études écologiques des traits de personnalité est de valider les tests comportementaux utilisés pour mesurer la personnalité, en les mettant en relation avec le comportement des animaux dans leur milieu naturel (Réale *et al.*, 2007).

Les animaux peuvent non seulement montrer des niveaux d'activité ou d'exploration différents, mais aussi montrer des manières distinctes de faire face au stress. Ainsi, lorsqu'ils sont soumis à un stress (par exemple lorsqu'ils sont placés dans un nouvel environnement), les individus peuvent exprimer différents niveaux de proactivité (Koolhaas *et al.*, 1999). Plus un individu est proactif, plus il réagit à un stress en tentant de contrôler activement sa source (Koolhaas *et al.*, 1999; Sluyter *et al.*, 1996). De plus, la proactivité semble reliée a une réponse plus rigide des individus face à un stress, basée sur des comportements qui dépendent de facteurs internes (Koolhaas *et al.*, 1999). Ces différences de proactivité entre les individus

sont également reliées à des différences physiologiques (revues dans Koolhaas *et al.*, 1999). Par exemple, la proactivité est reliée à une augmentation de l'activité du système sympathique et une activité du système parasympathique réduite; ce qui se traduit par un niveau de noradrénaline sanguine plus important et un rythme cardiaque plus élevé lors d'un stress. Le niveau de proactivité est aussi inversement relié à l'activité de l'axe hypothalamo-hypophysaire-surrénalien lors d'un stress, ce qui se traduit par des niveaux de corticostérone plus faibles et des niveaux de catécholamines plus élevés. Les individus plus proactifs ont aussi un niveau basal de testostérone supérieur, ce qui est relié à leur agressivité plus importante (Koolhaas *et al.*, 1999). En d'autres termes, lors d'un stress, les individus proactifs mobilisent leur énergie pour contrôler activement la source du stress (ex : risque, ou nouveauté), alors que les individus peu proactifs (dits aussi réactifs) mobilisent leurs ressources plutôt pour minimiser les conséquences négatives du stress.

I.4 Mesures des différences d'activité et d'exploration par un test d'arène

On quantifie le niveau d'activité et d'exploration d'un individu par un test d'arène, mesurant la réponse comportementale des individus dans un environnement nouveau (Archer, 1973; Walsh et Cummins, 1976). Les études réalisées sur des populations sauvages suggèrent que l'activité et l'exploration sont difficiles à départager à l'aide de ce test mais qu'il est robuste aux variations environnementales et peut être efffectué dans des conditions naturelles (Boon, Réale et Boutin, 2007; Martin et Réale, 2008). Le niveau d'activité et d'exploration d'un individu dans l'arène est par ailleurs représentatif de son comportement en nature. Par exemple, chez la mésange charbonnière (*Parus major*), les individus les plus actifs/explorateurs dans un environnement nouveau ont une propension plus importante à se disperser à partir de leur site de naissance (Dingemanse *et al.*, 2003). Chez l'écureuil roux (*Tamiasciurus hudsonicus*), les individus plus actifs et explorateurs lors d'un test d'arène sont capturés plus loin de leur territoire, et à des points de capture plus éloignés les uns des autres (Boon, Boutin et Réale, 2008). Ces différences d'activité et d'exploration entre les individus peuvent également avoir des répercussions sur des processus à plus grande échelle, comme

par exemple en permettant la colonisation d'environnements nouveaux (Duckworth et Babyaev, 2007).

Dans un environnement nouveau, il est possible que les individus montrent des différences au niveau de leur patron temporel d'activité et d'exploration. Par exemple, on s'attend à ce que plus un individu soit proactif, plus il montre une activité importante au début du test d'arène et diminue rapidement son activité avec le temps (Campbell *et al.*, 2003). La relation entre le niveau global d'activité et d'exploration et la réponse temporelle des individus à un environnement nouveau reste cependant peu étudiée. Si les individus testés ont tous le même patron temporel d'activité et d'exploration lors d'un test d'arène, alors une mesure du niveau global d'activité et d'exploration sur la totalité du test est un indice satisfaisant du niveau intrinsèque d'activité et d'exploration des individus. Par contre, si les individus montrent des patrons temporels différents, la durée du test peut influencer la relation entre le niveau global d'activité et d'exploration et son patron temporel. Par exemple, si les individus diffèrent au niveau de leur proactivité, on s'attend à ce qu'ils montrent des patrons temporels d'activité et d'exploration différents. En particulier, plus un individu est actif au début du test, plus son activité devrait diminuer au cours du temps. Un test relativement court devrait donc mener à une relation positive entre niveau global d'activité et le niveau d'activité au début du test. Si, au contraire, le test est plus long, on s'attend à ce que les individus les plus actifs en début de test soient ceux qui obtiennent le score global d'activité le plus faible, parce que les individus les plus actifs au début du test diminuent fortement leur activité au cours du temps.

I.5 Espèce modèle : le tamia rayé (*Tamias striatus*)

Le tamia rayé est un rongeur de la famille des sciuridés. On le retrouve en Amérique du nord surtout dans les forêts de feuillus relativement fermées, mais il occupe également des habitats plus ouverts ou des forêts matures. Son aire de distribution est importante, allant du lac Manitoba jusqu'aux côtes du Québec, s'arrêtant au nord de l'île d'Anticosti et s'étendant au sud jusqu'au golfe du Mexique (Snyder, 1982). Le tamia rayé se nourrit principalement de graines, de glands et de noix (Elliott, 1978; Snyder, 1982). Des insectes, des champignons et

le tubercule de certaines herbacées peuvent aussi faire partie de son alimentation (Landry-Cuerrier, 2008; Snyder, 1982). Le tamia survit l'hiver dans un terrier d'une profondeur pouvant aller de 20 cm à 1 m (Thomas, 1974), contenant une provision de graines et de noix accumulées durant l'été. Il exprime de la torpeur de manière à diminuer ses besoins énergétiques durant l'hiver (French, 2000; Scott et Fisher, 1972). Le tamia rayé peut utiliser un domaine vital relativement circulaire et symétrique, qui est centré autour du terrier et pouvant faire jusqu'à 55 m de diamètre (Yerger, 1953). Ces caractéristiques en font un sujet d'étude facile à capturer, à observer et à suivre sur plusieurs années.

Les accouplements peuvent avoir lieu au printemps (en mars), et à l'été (en juin) (Snyder, 1982; Wrigley, 1969; Yahner, 1978; Yahner et Svendsen, 1978), mais certaines femelles encore gravides ont été capturées en octobre, laissant penser qu'une reproduction est possible en automne (Smith et Smith, 1975). Les populations situées plus au nord de l'aire de distribution ne se reproduisent cependant qu'une seule fois par année. Pendant la saison de reproduction, les mâles sortent de leur domaine vital pour visiter les femelles avoisinantes. Ces visites devraient permettre aux mâles de sonder la réceptivité des femelles, déterminer la date de leur œstrus, et acquérir des informations sur leur propre territoire. Ces visites se traduisent par une utilisation plus importante du territoire par les mâles que les femelles (Elliott, 1978; Yerger, 1953). L'œstrus des femelles est court (environ 8h), relativement synchrone (la majorité des femelles entrent en œstrus sur une période de 4 à 5 semaines), durant lequel les mâles se rassemblent sur le territoire de la femelle et tentent activement de copuler avec elle. Certains mâles expriment un comportement de garde de la femelle, tentant par des comportements agressifs d'en restreindre l'accès par les autres mâles, tandis que d'autres semblent rester plutôt en périphérie du territoire de la femelle, minimisant ainsi les interactions avec les autres mâles (Elliott, 1978; Smith, 1968). Durant son œstrus, la femelle copule avec plusieurs mâles, mais beaucoup d'entre eux participant à la chasse de reproduction ne parviennent pas à féconder la femelle. Après une période de gestation d'environ 30 jours, la femelle donne naissance à une portée pouvant comprendre entre 2 et 7 jeunes (3 en moyenne). Les jeunes passent les premiers 30 à 45 jours dans le terrier maternel avant d'émerger et de se disperser pour trouver un terrier (Smith, 1968).

Le système de reproduction du tamia rayé est une forme de promiscuité (certains auteurs le décrivent également comme une forme de polygynie) où les mâles sont principalement en compétition indirecte pour les femelles. Ce système de reproduction, allié à la facilité de capture des tamias, offre une opportunité intéressante d'étudier les caractéristiques susceptibles d'affecter le comportement reproducteur et le succès de reproduction des mâles. Les observations réalisées durant les accouplements chez cette espèce nous laissent penser que les mâles varient de manière importante dans leur comportement de reproduction. Enfin, il est possible et relativement facile de quantifier l'activité et l'exploration des individus chez le tamia rayé, comme le démontre une étude antérieure (Martin et Réale, 2008).

I.6 Objectifs de ce mémoire

Ce mémoire se veut une étude écologique tentant de mieux comprendre le lien entre l'utilisation de l'espace par les mâles pour se reproduire et leur personnalité, en tenant compte des facteurs environnementaux. Mon objectif est dans un premier temps de préciser la nature des différences de personnalité mises en évidence par le test d'arène en utilisant une méthode permettant de prendre en compte le patron temporel d'activité et d'exploration des individus (Réale *et al.*, 2007). Comme mentionné précédemment, la relation entre le niveau global et le patron temporel d'activité et d'exploration des individus durant le test reste encore à préciser. J'utiliserai des modèles linéaires généralisés mixtes pour analyser le comportement des individus dans l'arène. Je m'attends à ce que le patron temporel d'activité et d'exploration dans l'arène varie d'un individu à l'autre. Mon deuxième objectif est de déterminer si le niveau d'activité et d'exploration des individus affecte l'utilisation de l'espace par les mâles pendant la reproduction (qui est potentiellement reliée au comportement de recherche de partenaires sexuels). Pendant la reproduction, les mâles devraient utiliser une surface plus importante que les femelles. En dehors de la saison de reproduction, je m'attend plutôt à ce que les mâles et les femelles utilisent une surface similaire. Enfin, le niveau d'activité d'un mâle devrait être relié à la surface qu'il utilise durant la reproduction.

CHAPITRE I : INDIVIDUAL VARIATION IN TEMPORAL ACTIVITY PATTERNS AND THE MEASUREMENT OF ACTIVITY/EXPLORATION IN AN OPEN-FIELD TEST IN THE EASTERN CHIPMUNK (*TAMIAS STRIATUS*)

Pierre-Olivier Montiglio, Dany Garant, Don Thomas, et Denis Réale; à soumettre.

RÉSUMÉ

Les différences individuelles d'activité forment la base des traits de personnalité, et sont mesurés par des tests d'arène. Durant ces tests, les individus peuvent ajuster leur niveau d'activité avec le temps. Si les individus diffèrent au niveau du patron temporel d'activité, les résultats du test d'arène seront biaisés par la durée du test. Nous avons utilisé des modèles généralisés mixtes sur le temps d'activité durant les tests d'arènes pour surmonter ces problèmes potentiels, corriger l'effet de facteurs environnementaux et estimer la reproductibilité des scores d'activité ainsi que du patron temporel d'activité de tamias rayés (*Tamias striatus*). Nous avons détecté des différences au niveau du patron temporel d'activité des individus en accord avec un gradient de proactivité. Le score global d'activité ainsi que son patron temporel étaient reproductibles. La proactivité des individus était positivement reliée au score global d'activité. Nos estimés de reproductibilité étaient similaires à ceux obtenus chez d'autres populations de sciuridés. Nos résultats démontrent que les études utilisant des tests d'arènes doivent prendre en compte le patron temporel d'activité et le score d'activité global pour permettre la validation des traits de personnalité en milieu naturel.

ABSTRACT

Individual differences in activity and exploration in a novel environment constitute the basis of animal personality and are measured during an open-field test. During open-field tests, individuals may change their activity/exploration level (AEL) with time. If individuals differ in their temporal pattern of AEL, then the reliability and the meaning of global AEL scores will be affected by the duration of the test. We present a method to circumvent the potential problems that stem from inter-individual differences in temporal activity patterns during open-field tests analyses. We ran generalized linear mixed models on the time spent active/exploratory during open-field tests on eastern chipmunks to correct for environmental effects and estimate repeatability of global AEL and of its temporal variation. We detected individual differences in the temporal AEL pattern that matched the proactivity gradient. Global AEL and its temporal variation were repeatable. Proactivity was positively linked to global AEL. Our repeatability estimates were similar to those obtained previously in other populations of sciurids. Studies using open-field tests should take into account the temporal variation of behaviours in the open-field as well as the global AEL to help interpret and validate personality traits in the wild.

Keywords: activity, exploration, coping styles, open-field test, personality, *Tamias striatus*.

1.1 INTRODUCTION

Psychological and ecological studies on animal personality consider a novel environment as stressful for the individual, meaning that we expect this situation to elicit behavioural or physiological responses from animals. These responses have been studied from a mechanistic as well as an evolutionary point of view, and we consider that they enable the individual to cope with the environment in order to maintain homeostasis (Martí and Armario, 1998; Selye, 1956). The test that is most widely used to study the response of animals to novelty is the open-field test, where individuals are subjected to a neutral arena (Archer, 1973). Based on the assumption that individuals have to move and express diverse behaviours (for example climbing/sniffing the walls, move around) in order to explore the arena, studies have used time spent active by individuals during open-field tests as a measure of their intrinsic activity and exploration level (AEL) (Archer, 1973; Martin and Réale, 2008; Walsh and Cummins, 1976). We are now aware that individuals of the same population often show consistent differences in their activity and exploration level, and that these differences form the basis of animal personalities (Réale *et al.*, 2007). Earlier studies in wild populations have shown that behaviour in the open-field is repeatable (i.e. individuals behave in a consistent manner across replicated tests), and that activity and exploration are difficult to separate experimentally (Boon, Réale and Boutin, 2007; Martin and Réale, 2008).

When subjected to the same stressor repeatedly, however, individuals usually show a change in their response to the stressor, a phenomenon frequently referred to as habituation (however habituation can have a narrower meaning, e.g. Lachuer *et al.*, 1994). The pattern of temporal response expressed by individuals to a repeated stress has been described for different tests, involving an array of stressors such as noise (Armario, Castellanos and Balasch, 1984), immobilization stress (Lachuer *et al.*, 1994), and novelty (Boon, Réale and Boutin, 2007; Martin and Réale, 2008). This temporal change may result from (1) a decrease of emotional activation (the individual becomes more familiar with the stressor), and (2) a change in the

biochemical control of the response elicited by the stressor (for example, down-regulation of hormonal receptors) (Martí and Armario, 1998). Individuals may change their response pattern from one occurrence of the stressor to the other (for example, repeated exposure to noise may elicit a decrease in the physiological response over successive trials in rats, Armario, Castellanos and Balasch, 1984). Similarly, when individuals experience a stress for a continuous time interval, they may change their response over time. For example, mice show changing levels of activity during the course of one open-field test (Kalueff, Jensen and Murphy, 2007). To avoid the confusion with the term "habituation" used in psychology, we will refer to this change in the response of individuals during tests as the "temporal pattern" of the response.

The temporal pattern of the response expressed by individuals in a novel environment (for example an open-field test) may vary from one individual to the other because individuals may cope with the stressful situation in different ways (i.e. they may express different coping styles, sensu Koolhaas *et al.*, 1999). Previous work on coping styles show that individual coping styles can be organized over a continuum of proactivity. At one extreme of the continuum, highly proactive individuals respond to the stressor by actively manipulating it. At the other extreme, individuals with a low proactivity express avoidance-based behaviours (Carere *et al.*, 2005; Koolhaas *et al.*, 1999; Sluyter *et al.*, 1996). Individuals along the proactivity gradient vary in a vast array of behavioural and neuro-physiological traits, but a general pattern is discernible. Indeed, proactivity seems to be associated with behaviours driven by internal factors, and the higher the proactivity level of an individual, the less we expect its behaviour to be affected by external stimuli (i.e. more proactive individuals will express more rigid behaviours) (Benus, Bohus and Van Oortmerssen, 1991; Koolhaas *et al.*, 1999). Proactivity is generally positively related with boldness, aggressiveness (Benus, Koolhaas and Van Oortmerssen, 1992; Boon, Boutin and Réale, 2008; Boon, Réale and Boutin, 2007; Van Oortmerssen and Bakker, 1981), and the tendancy to develop fixed behavioural patterns when subjected repeatedly to a given learning task (i.e. they form routine-like behaviours, Benus, Koolhaas and Van Oortmerssen, 1987; Marchetti and Drent, 2000). Proactivity is also negatively related to the time to recover from a defeat resulting from a social interaction (Carere *et al.*, 2001).

Individuals along a proactivity continuum are expected to express different temporal patterns in their response during open-field tests. For example, in a study by Campbell *et al.* (2003), more proactive individuals initiated exploration of a novel environment more rapidly but tended to show an abrupt decrease in exploration over time. On the contrary, individuals with a lower proactivity had a greater latency to initiate exploration, but maintained a prolonged activity and exploration level over time. Such temporal patterns of AEL suggest that a higher proactivity level may be related to faster, but more superficial exploration tactics.

If individuals express different temporal patterns of AEL as a result of their coping style (Benus, Bohus and Van Oortmerssen, 1991; Koolhaas *et al.*, 1999), then the reliability and the meaning of AEL will be affected by the duration of the test. Open-field tests usually vary in duration. Some open-field tests have been conducted over time intervals of up to 30 minutes (Duffy *et al.*, 2008; Helms *et al.*, 2008) or even 1 hour in mice (Elder *et al.*, 2008; Pietropaolo, Feldon and Yee, 2008). On the other hand, some studies used shorter open-field tests, based on the idea that the first minutes during which individuals are subjected to the novel environment (the beginning of their temporal pattern of activity) captures most of the inter-individual differences in activity and exploration as well as their proactivity. Examples of such studies include open-field tests conducted on red squirrels (*Tamiasciurus hudsonicus*) by Boon, Réale and Boutin (2007) that lasted 7 minutes, and open-field tests conducted on eastern chipmunks (*Tamias striatus*) by Martin and Réale (2008), that lasted 5 minutes. Shorter open-field tests should be preferred when conducted on wild animals, has they generate less logistic problems (time is usually limiting during field work sessions), and minimize the stress and manipulation load exerted on animals. However, most laboratory studies do not give any justification for the duration of the open-field test, and some studies focused their interest on the global activity level only (Kalueff, Jensen and Murphy, 2007; Walsh and Cummins, 1976).

The global AEL score and coping style expressed by a given individual has repeatedly been shown to be consistent across time, and most studies on wild/unselected animal populations suggest a continuous inter-individual variation in those traits (Boon, Réale and Boutin, 2007;

Carere *et al.*, 2005; Martin and Réale, 2008). We thus expect consistent individual differences in both global AEL and temporal pattern of AEL between tests, and so the effect of the duration of the open-field on the relationship between global AEL and its temporal pattern should be systematic. If the individuals that show a higher activity level at the beginning of the test, also show a steeper decrease in activity over time than others (Fig. I-1 (1)), we expect individuals with a higher AEL at the beginning of the test to obtain a lower global AEL (Fig.I-1 (2)). But if activity is considered on a shorter time interval (Fig I-1 (3)), we expect individuals with a higher AEL at the beginning of the test to obtain higher global AEL (Fig. I-1 (4)). The duration of the test will thus affect the relationship between global AEL and the temporal pattern of AEL.

In this study, we present a method to circumvent the potential problems that stem from inter-individual differences in the temporal pattern of activity and exploration over the duration of open-field tests, using open-field tests conducted in a wild eastern chipmunk population over two years. We show how the occurrence of individual differences in the temporal pattern of activity may be detected and accounted for by using Generalized Linear Mixed Models (GLMM) to analyze AEL temporal patterns and show that open-field tests with relatively short durations provide a reliable indication of individual activity/exploration levels even if individuals differ in the temporal pattern of their response during open-field tests. This method will enable a clearer description of the individual's responses to open-field tests and thus a better assessment of differences in personality traits between individual. Our study is therefore a necessary step for ecological studies of animal personality aiming at validating measurements of open-field tests as a measure of personality.

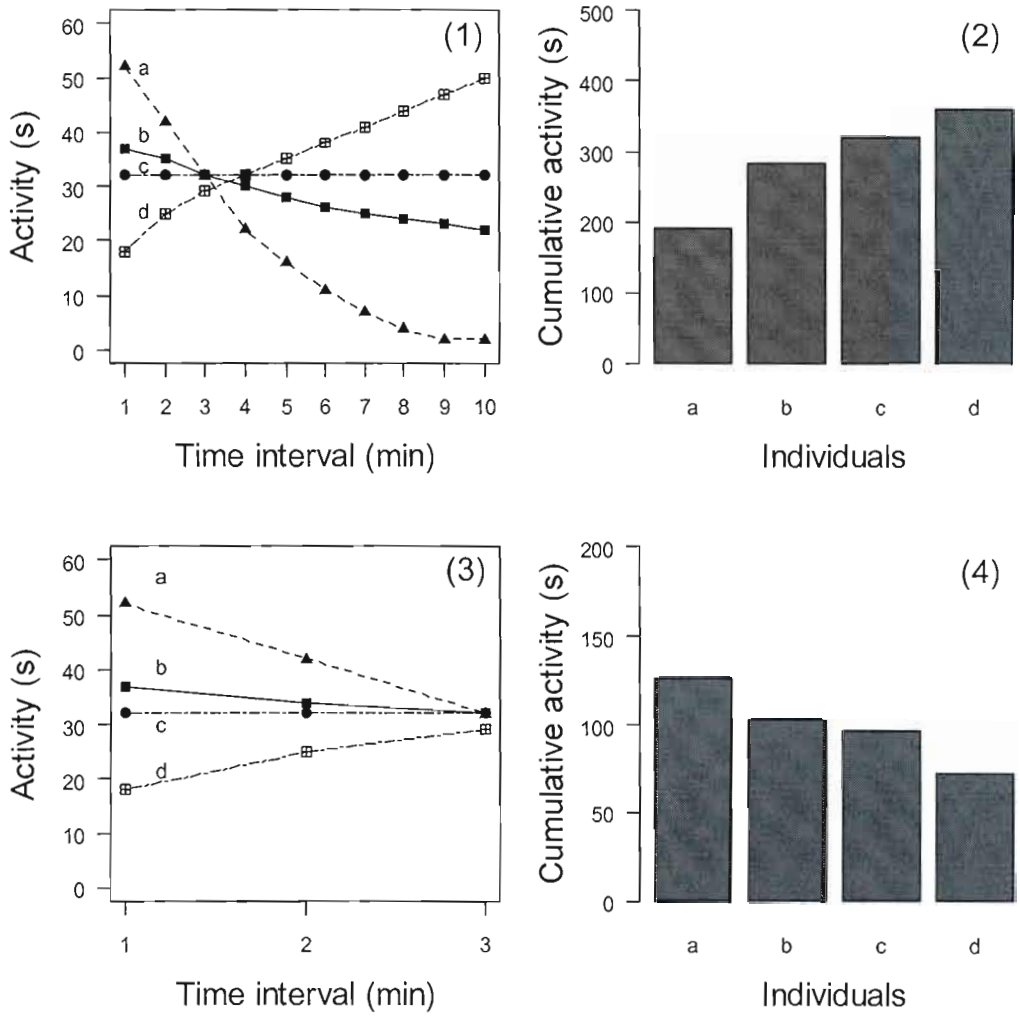

Figure I-1 Hypothetical activity/exploration level of four individuals ("a", "b", "c" and "d") showing a continuous variation in the temporal pattern of their response to an open-field test conducted over a time period of 10 minutes (1). The relationship between the activity shown by an individual during the first minute and its global activity/exploration score will be negative (2). If activity is measured over a shorter time interval (3), the relationship will be reversed (4).

1.2 METHODS

Model species, study site, live trapping and burrow location

Eastern chipmunks are ground dwelling sciurids found mostly in deciduous wooded areas of eastern North America. They are also found in more open and bushy habitats, as well as mature forests (Snyder, 1982). Chipmunks are central place foragers that feed mostly on seeds, nuts and acorns. They may also prey on invertebrates such as insects (Snyder, 1982) and consume spring beauty tubers (Landry-Cuerrier, 2008).

The study site is a 500 x 500 m flagged grid located in southern Quebec, Canada (45°05' N; 72°25' W), in a semi-closed deciduous forest where sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) dominate. We live-trapped individuals from May to November in 2006 and 2007, using 255 Longworth traps (Longworth Scientific Instruments Ltd, Abingdon, UK). At the first capture, we marked individuals with two metal ear tags (National Band and Tag Co., New York, KY), and one unique Trovan PIT tag (Eidap Inc., Alberta, Canada). We also recorded the sex and reproductive status (based on nipple size/aspect for females and testis position for males). Individuals were weighted to the nearest gram with a Pesola spring balance (Science Import Inc., Quebec, Canada). Age class (juvenile or adult) was determined according to body weight at first capture and reproductive status (individuals captured below 70 g that did not reproduce were considered juveniles).

Open-field tests

We quantified activity-exploration using an open-field test (see Archer, 1973; Dingemanse *et al.*, 2003; Martin and Réale, 2008 for a detailed description of the test). Open-field tests were conducted on the grid from May to November in each year to test individuals in various

reproductive states. Once captured, chipmunks were carried in the trap from their capture location to the open-field arena (distance ranging from 15 to 250 m; mean = 131.8 ± 85.7). Briefly, the arena consisted of a rectangular white plastic box (80x40x40 cm) with a Plexiglas lid. We used a modified version of the open-field apparatus that included holes on the bottom (i.e. a hole board). The number of times individuals inspect holes during a hole board test is a reliable measure of exploration (File and Wardill, 1975). Animals were allowed to rest for 3 min in the trap without any movement. They were taken gently out of the trap, transferred to a manipulation mesh bag, and then transferred to a PVC chamber connected to the arena without any direct manipulation (see Fig. I-2). They were gently pushed inside the arena, where their behaviour was recorded for 3 min using a Sony Camcorder placed above the arena. The experimenter remained silent and was not visible to the chipmunk during the test.

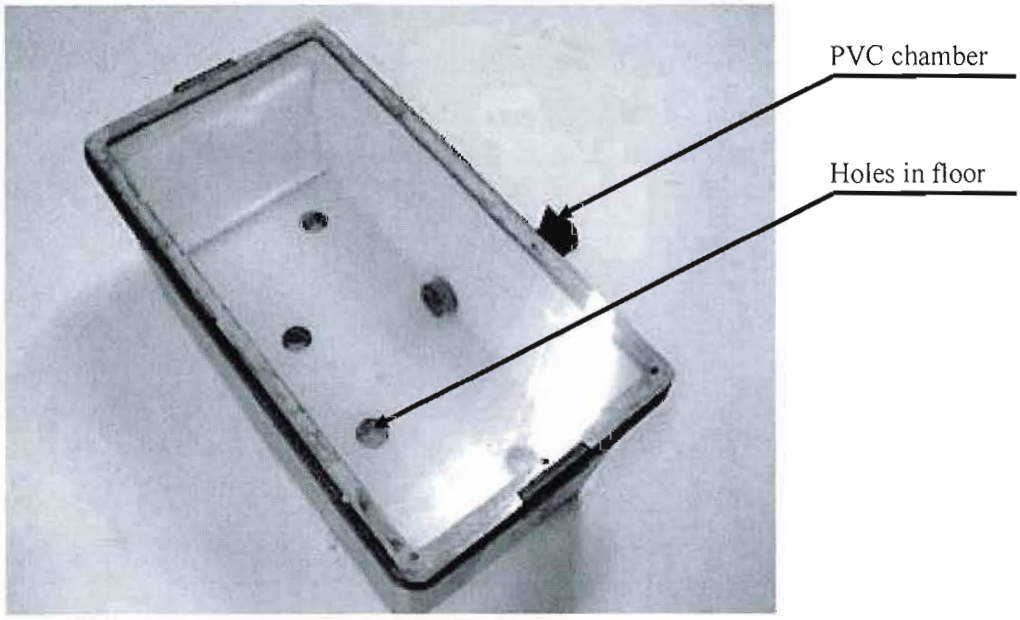

Figure I-2 Arena used for the open-field tests. The chipmunks are transferred to the PVC chamber before being pushed gently inside the area, where holes have been cut into the floor.

Activity and exploration measurements

As the response of individuals may decrease across repeated trials (Martin and Réale, 2008), successive open-field tests conducted on a given chipmunk were spaced by a minimum of 15 days. Chipmunk behaviours during the test were scored using the software The Observer (Noldus Inc.) and the ethogram derived from Martin and Réale (2008). We computed the number of seconds where the individual was active (i.e. when it was expressing any of the behaviours listed in Table I-1, except immobility).

Table I-1 Behaviours recorded on chipmunks during an open-field test. Scanning, locomotion, head dipping, hanging and rear were used to compute the time spent active by chipmunks in the open-field.

Behaviour	Description
Scanning	Repeated changes in the orientation of the head, without any locomotion.
Locomotion	Movement of the whole body, includes short scanning bouts of less than 0.5 seconds.
Head dipping	Inspections of the holes cut in the floor of the arena, noticeable by quick movement of the head and/or anterior part of the body forward, inside the hole.
Hanging	Escape attempts where the individual jumped and stayed near the top of the arena, in contact with the lid.
Rear	Standing position, on the hind limbs only, usually with rapid scanning movements of the head.
Immobility	Still, with four paws on the ground.

Statistical analysis

All statistics were done using the software R 2.7.1 (R Development Core Team 2008). To assess individual consistency of behaviour in the open-field, we ran generalized linear mixed models (GLMM, Pinheiro and Bates, 2000) on time spent active with a quasi-Poisson

distribution. All GLMM on time spent active used the following variable as the response: 180 – y, where y is the number of seconds spent active during open-field test. All results and effect sizes presented in this study were back transformed to ease interpretation. We used only individuals that were tested twice. In order to assess consistency across years and age cohorts, separate models were built for the adults tested in 2006, the naïve adults in 2007 and the juveniles tested in 2007. Chipmunk identity was used as a random effect, and the explanatory variables included in the initial models were age class, sex and trial order (first vs. second test). We also included transportation distance and number of captures in all the models, to control for potential effects of distance moved from the trapping area to the open-field and the history of capture of an individual on its behaviour in the open-field. The model was simplified by backward stepwise deletion until all the remaining terms were significant (i.e. selected model).

We could not test whether the variance component related to chipmunk identity was significantly different from 0. Testing such variance components is usually done by using a log-likelihood ratio test (one degree of freedom) between the selected model including the random effect of interest (in our case chipmunk identity) and a model without it but with the same fixed effects (Pinheiro and Bates, 2000). However, no likelihood calculation methods currently exist for this kind of model. We computed r, or the repeatability estimates, as the ratio of the variance component related to the intercept of the random effect (Vi) on the sum of the variance component related to the intercept (Vi) and the residual variance (Vr). Thus r = (Vi)/(Vi+Vr).

In order to analyse the dynamics of behaviour changes within the test we calculated the time spent active for three 60-seconds intervals. We then used the same model as described above but with time interval (0 to 60 s, 60 to 120 s and 120 to 180 s) added as an additional fixed effect (continuous variable). Time spent active was transformed as above and we present back-transformed results and BLUPs. We estimated individual elevation and individual slopes in activity by fitting both individual identity and the interaction between time interval and individual identity as random effects. Significance of chipmunk identity (random effect over the intercept) was assessed by a log-likelihood ratio test (described above) between the

model including the interaction between individual identity and time interval (i.e. a model including a random effect over the intercept and a random effect over the slope), and a model without any random effect on the intercept (i.e. a model with only a random effect over the slope).

We also fitted two final models using data pooled over the two years and the same explanatory variables as for age cohorts models to compute the *Best Linear Unbiased Predictors* (BLUPs, Pinheiro and Bates, 2000) as a measure of individual behavioural profile (see Martin and Réale, 2008). In the total duration model, a single BLUP value was computed for each chipmunk and represented the individual deviation from the common (group) intercept (elevation, sensu Nussey, Wilson and Brommer, 2007). In the time interval model two BLUP values were computed. These two values represent the individual deviation from the intercept and the individual deviation of the common slope (i.e. changes in activity with time) relative to the general slope of the model.

To test significance of the fixed effects parameters in the time interval and the total duration models, we conducted Markov-chain Monte Carlo simulations (1 chain, n = 50000). The simulations enabled us to compute a 95% confidence interval for each fixed effect parameter included in the models (Bates, personal communication).

Using BLUP values from the time interval model, we tested whether the correlation between individual intercepts (estimated activity/exploration level of chipmunks during the first minute of the test) and slopes (change in activity/exploration over the duration of the test) was negative, to test if individuals express different dynamics of behaviour through time. The decrease in activity of less active individuals is constrained by a minimum (null) activity score (i.e. individuals cannot express negative activity scores). This constraint could result in a negative correlation between individual intercept and slope even if chipmunks did not express patterns predicted by the coping style approach, because less active individuals are not able to decrease their activity as much as more active individuals. To test for this potential artefact, we divided the range of BLUPs related to the intercept from the time interval model to create three groups of chipmunks with varying temporal activity patterns.

We computed the mean activity level during the third minute of the less active group (negative BLUP values, less proactive individuals) to test if chipmunks with low activity at the beginning of the test were still active at the third minute. An artefact resulting from the constrained slope of less proactive individuals could be invoked only if these individuals were completely inactive at the third minute of the test. We also tested the correlation between the BLUPs related to the intercept an individual obtained from the time interval model (i.e. its activity/exploration level during the first minute of the test) and the total duration model (i.e. its global activity/exploration level during the three minutes of the test), to test for the similarity between the two measures.

1.3 RESULTS

Open-field tests and individual consistency

We ran 274 open-field tests in 2006 and 150 in 2007. We repeated the open-field test twice on 71 individuals. Mean number of seconds of activity/exploration for each time interval and trial are presented in Fig. I-3. Overall, chipmunks tended to decrease their activity and exploration level over time. However, even if most of the individuals decreased their activity, some of them increased it. As an example, activity/exploration level averaged between trials is presented for three individuals in Fig. I-4. Effect sizes of selected models for each cohort and for pooled data are reported in Table I-2 for total duration models and in Table I-3 for time interval models (all rejected variables, $p > 0.2$). Repeatability estimates of selected models are reported in Table I-4. Repeatability estimates computed for each age cohort for the total duration model ranged between 33 and 53% and were similar to the final estimates computed for pooled data (Table I-4). Similarly, repeatability estimates computed from the time interval models were close to the estimate from the time interval model with pooled data. Variance components related to chipmunk identity (random effect on the intercept) from the time interval model were higher (85% of the total variance for the pooled data) than the estimates from the total duration model (46% of the total variance for the pooled data). All

variance components related to the intercept (chipmunk identity) in the time interval models were significantly different from 0% (Table I-4).

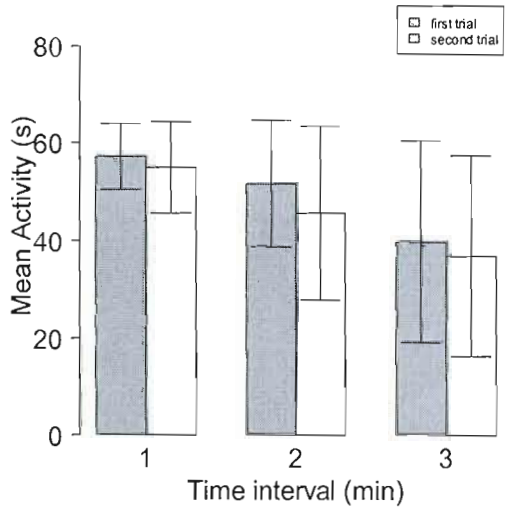

Figure I-3 Mean number of seconds (± s.d. of the mean) spent active for eastern chipmunks during the first and second open-field test. Tests were separated in three time intervals of 60 seconds each.

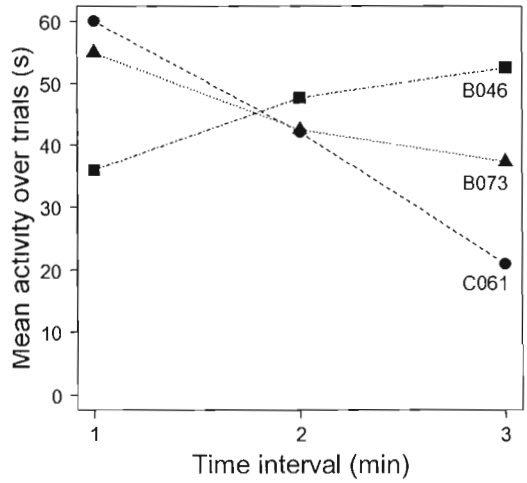

Figure I-4 Mean activity level of 3 individuals from our study ("B046", "B073", "C061"). Note that all individuals are still active at the end of the test.

Overall, we detected a significant decrease in global AEL between the first and second trial (pooled data: coefficient = -0.34; 95% CI = [-0.39; -0.28]). However, this decrease was not significant for adults and juveniles in 2007 (Table I-2). Sex, number of captures, and transportation distance were rejected from the total duration models.

The time interval model including all the individuals with replicated tests in 2006 and 2007 showed a significant decrease in activity/exploration between successive trials (pooled data: coefficient = -0.38; 95% CI = [-0.44; -0.32]), and within tests (pooled data: coefficient = -0.02; 95% CI = [-0.02; -0.01]). It is important to note that even if the majority of the individuals decreased their activity level with time during an open-field test, some increased it: adding the BLUPs related to the slope to the effect size of time interval in the time interval models yields slopes ranging from negative to positive values (range: -0.046; 0.013). We found a significant effect of chipmunk identity (see Table I-4 for log-likelihood ratio tests of time interval models) indicating that individual differed significantly over their initial activity/exploration (pooled data: r = 85.69%; $\chi^2 = 825.58$; $p < 0.0001$; see Table I-4). Sex, number of captures, and transportation distance were rejected from the models (all $p > 0.4$).

Time interval was non-significant for juveniles in 2007, potentially due to the limited sample size (N = 6). Because the parameter in the juvenile model was similar to the other cohorts, we chose to keep it in the model. This enabled us to compare all three cohorts on the same basis.

Global activity level and activity patterns

BLUPs of individual intercepts and slopes from the time interval model were strongly negatively correlated ($r = -0.895$, $p < 0.001$; Fig. I-5). Hence, individuals showing a high AEL at the beginning of the test also had a steeper decrease in AEL across time intervals. BLUPs related to the intercept from the time interval model with pooled data ranged between –3.80 and 5.20. Thus dividing this range in three equal intervals resulted in groups with individual BLUPs ranging between –4.10 and –1.00 (low proactivity individuals, N = 30), -1.00 and 2.10 (average individuals, N = 29), and 2.10 and 5.20 (high proactivity individuals, N = 12). The mean number of seconds spent active by chipmunks of the low proactivity group was 35.16 (range: 0; 60). 63% of the individuals in this group were active during more than 10 seconds during the last minute of the test.

BLUPs of individual intercepts from the time interval model were positively correlated with BLUPs of individual intercepts from the total duration model ($r = 0.354$, $p = 0.002$; Fig. I-6). Individuals showing a high AEL at the beginning of the test thus tended to spend more time active over the whole test.

Table I-2 Fixed effects of selected models for chipmunk activity for the total duration of the test in open-field of each cohort in 2006 and 2007. Coefficients are given ± the 95% confidence interval based on Markov-chain Monte Carlo simulations. All models include chipmunk identity as a random effect on the intercept.

	Adult 2006 (N = 41)	**Adult 2007** (N = 11)	**Juveniles 2007** (N = 6)	**Pooled data** (N = 71)
Factor	Coefficient (95% CI)	Coefficient (95% CI)	Coefficient (95% CI)	Coefficient (95% CI)
Intercept	**-2.83** (-3.14; -2.50)	**-3.45** (-3.96; -2.85)	**-2.82** (-3.80; -1.29)	**-2.80** (-3.07; -2.56)
Trial order	**-0.33** (-0.40; -0.26)	Rejected	Rejected	**-0.34** (-0.39; -0.28)

Variables initially included in the models as fixed effects were age class (pooled data only), sex, trial order (first vs. second test), transportation distance and number of captures.

Table I-3 Fixed effects of selected models of activity by time intervals in open-field of each cohort in 2006 and 2007. Coefficients are given with 95% confidence intervals. Time interval did not have a significant effect on juvenile activity in 2007 but was kept in the model to facilitate comparisons between cohorts. All models include an interaction between chipmunk identity and time interval as a random effect.

	Adult 2006 (N = 41)	**Adult 2007** (N = 11)	**Juveniles 2007** (N = 6)	**Pooled data** (N = 71)
Factor	Coefficient (95% CI)	Coefficient (95% CI)	Coefficient (95% CI)	Coefficient (95% CI)
Intercept	**1.21** (0.20; 2.32)	**0.54** (-1.81; 3.33)	**0.72** (-4.05; 7.10)	**-0.94** (-1.62; -0.34)
Trial order	**-0.39** (-0.46; -0.31)	Rejected	Rejected	**-0.38** (-0.44; -0.32)
Time interval	**-0.02** (-0.02; -0.01)	**-0.02** (-0.02; -0.01)	-0.02 (-0.05; 0.16)	**-0.02** (-0.02; -0.01)

Variables initially included in the models as fixed effects were age class (pooled data only), sex, trial order (first vs. second test), time interval, transportation distance and number of captures.

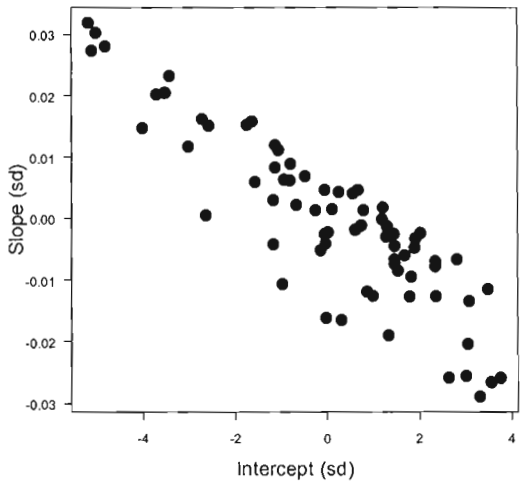

Figure I-5 Relationship between BLUPs related to the intercept (initial activity) and the BLUPs related to the slope of activity/exploration from the time interval model for 2006 and 2007. BLUPs are expressed as standard deviations from the common parameter estimate (intercept and slope). Active individuals are represented by positive values.

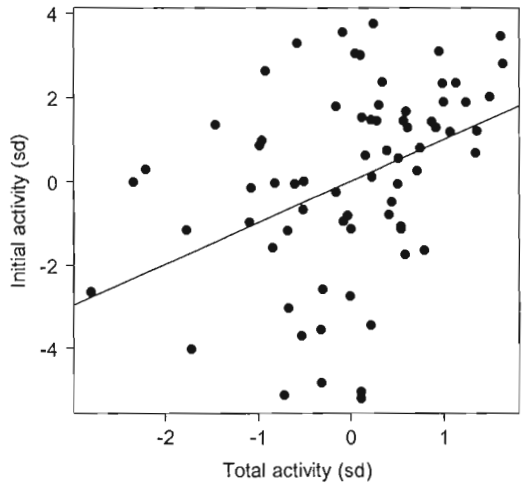

Figure I-6 Relationship between BLUPs related to the intercept from the time interval model (initial activity), and BLUPs related to the intercept from the total duration model (total activity) for 2006 and 2007. BLUPs are expressed as standard deviations from the common parameters (intercepts). The line has a null intercept and a slope of 1. Active individuals are represented by positive values.

Table I-4 Repeatability estimates for the open-field tests in 2006 and 2007. Time interval models included chipmunk identity and year as a random effect on the intercept, as well as an interaction between chipmunk identity and time interval. Total duration models included chipmunk identity and year as random effects on the intercept (variance components related to year are not shown in this table). Log likelihood ratio tests (χ^2) were all significant, indicating that variance component related to chipmunk identity were different from 0 in the time interval models as well as in the total duration models.

	Time interval models							Total duration models		
Cohorts	N	Vi	Vs	Vr	r	χ^2+	P value	Vi	Vr	r‡
adults 2006	41	47.06	0.0018	6.06	88.58%	462.08	< 0.0001	138.35	165.23	47.57%
adults 2007	11	58.95	0.0016	7.63	88.53%	178.69	< 0.0001	207.22	418.97	33.09%
juveniles 2007	6	29.54	0.0012	4.08	87.87%	45.18	< 0.0001	121.43	109.36	52.61%
pooled data	71	53.07	0.0020	8.89	85.69%	825.58	< 0.0001	177.47	194.47	45.57%

Vi = Individual variance; Vs = variance in the slope; Vr = residual variance; r = repeatability.

+ log-likelihood ratio test between a model with an interaction between chipmunk identity and time interval and a model without any random effect over the intercept (significant p values indicate the effect of chipmunk identity is significant). The interaction between chipmunk identity and time interval were all highly significant ($p < 0.0001$; results not shown).

‡ p values for repeatability estimates are not available because no log-likelihood ratio are currently available for the *lmer* function in R.

1.4 DISCUSSION

In this study, we show that individuals express a change in AEL during the course of the open-field test. The global AEL measured during the whole duration of an open-field test, as well as the temporal pattern of AEL shown by individuals, are both repeatable. Importantly, we detected a strong negative relationship between the initial AEL and the slope of the AEL, indicating that individuals that are more active at the beginning of the open-field test are also those with the stronger decline in AEL over the course of the test and vice versa. Thus, in this chipmunk population, individuals show consistent differences in the temporal patterns of activity and exploration level. These differences match the proactivity gradient described in the literature and a test with a short duration (3 minutes in our study) is able to detect such inter-individual differences.

Our repeatability estimates (ranging from 33 to 53%) of global AEL are similar to those obtained previously in a different population of eastern chipmunks by Martin and Réale (2008) that ranged between 23 and 43%. Our estimates were also similar to the estimates reported by Boon, Réale and Boutin. (2007) for red squirrels (*Tamiasciurus hudsonicus*) using the same open-field methods that ranged between 37 and 68%. Repeatability estimates of activity and exploration in novel environments in less related species such as domestic mice (*Mus musculus*, 30%, Van Oortmerssen and Bakker, 1981) and great tits (*Parus major*, range: 27; 66%, Dingemanse *et al.*, 2002) are also comparable to our values. Thus, the stability of activity and exploration levels over time is a widespread phenomenon among animal populations. We detected a decrease in activity/exploration between successive trials, and this is consistent with most studies. Chipmunks did not seem to differ in the intensity of this decrease, and we are not aware of any evidence of such individual differences in the literature.

The majority (but not all) of the individuals we tested expressed a decrease in their AEL during the course of the test. At one extreme, some chipmunks responded to the novelty of

the open-field by actively trying to escape or explore, thereby showing a higher initial AEL (proactive style). At the other extreme, some chipmunks froze (i.e. reactive style). These differences in decrease may have profound implications on the meaning and validity of open-field tests, because, as the test gets longer, some individuals will eventually reach a minimum AEL at different rates. The length of the test may thus affect the variability observed between individuals. In cases in which individuals show a decrease in response to the test, we expect differences between individuals to be more obvious when shorter tests are used. In our study, we were able to quantify a consistent component of activity and exploration using a test of only 3 minutes.

As individuals showed different temporal activity/exploration patterns in the open-field, the global AEL during the open-field tests may be biased by the duration of the test. For example, in our study, individuals with a higher initial AEL were those with higher global AEL scores. With a longer test, however, individuals with a lower initial AEL but with a weaker decrease in activity may have obtained a higher global AEL score.

Our study aimed at validating short open-field tests (3 minutes) as a measure of inter-individual differences in activity/exploration, or coping styles. One may wonder if the negative relationship between activity during the first minute of the test and the intensity of the decrease in activity over time is a statistical artefact. We argue that such artefact cannot account alone for the many evidences that individual from a vast array of rodent species differ in their coping style, and that these differences translate into a negative relationship between initial activity and its change over time (Walsh and Cummins, 1976). However, because of the short duration of our tests, a limited number of points per individual (3) were available to fit a temporal trend. Three points are sufficient to detect any type of temporal pattern and we have no reason to expect a negative correlation between individual intercept and slope only on a statistical basis: individuals could have expressed a decrease, an increase or no temporal variation in activity, irrespective of their behaviour during the first minute of the test. Such an artefact could occur if (1) all individuals decreased their activity during the test and (2) if less active individuals had all stopped activity before the end of the open-field (i.e. their slope is constrained by the null activity score they would obtain). In our study, (1)

not all chipmunks expressed a decrease in activity (some individual actually obtained a positive slope of activity over time), and most (63%) of the individuals with a lower activity during the first minute (less proactive group, see results) were still active for more than 10 seconds by the end of the test.

Open-field tests used in studies in psychology and behavioural ecology are very variable in duration, with test durations ranging from 3 minutes (our study) to 1 hour for rodents (Elder *et al.*, 2008; Pietropaolo, Feldon and Yee, 2008). This large variation in the duration of the test can bias measurement of activity and exploration of individuals because they are likely to differ in the temporal activity and exploration patterns they express. In addition, the scale on which activity and exploration patterns occur may vary with the species studied. As a result, it is difficult to compare such studies and to validate traits measured in the open-field test, as the global AEL of individuals may have a different meaning from one study to the other. This potential bias may impede further ecological studies, for which a primary goal is to validate open-field measures of personality traits by relating these traits to the behaviour of individuals in their natural environment (Réale *et al.*, 2007). We thus recommend that future studies of personality traits should take into account and report the temporal activity and exploration patterns as well as the global level of AEL during open-field tests.

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CHAPITRE II : ACTIVITY/EXPLORATION DURING OPEN-FIELD TESTS, SPACE USE AND MATE SEARCH IN THE EASTERN CHIPMUNK (*TAMIAS STRIATUS*)

Pierre-Olivier Montiglio, Dany Garant, et Denis Réale; à soumettre.

RÉSUMÉ

Les mâles et femelles de beaucoup d'espèces expriment des comportements reproducteurs contrastés. Les femelles maximisent les ressources allouées à la reproduction et la qualité des partenaires, tandis que les tactiques masculines visent à maximiser le nombre de femelles fécondées. Chez plusieurs sciuridés, la recherche de partenaires sexuels prend place avant la saison de reproduction, les mâles visitant les femelles sur leurs domaines vitaux. Cette recherche peut être affectée par le niveau d'activité des mâles. Nous déterminons comment les différences individuelles d'activité entre les tamias rayés mâles (*Tamias striatus*) affectent leur utilisation de l'espace, qui représente un indice valable de la recherche de partenaires. Nos objectifs étaient de (1) comparer les domaines vitaux des mâles et femelles en période de reproduction et en absence de reproduction, et (2) de déterminer si la surface utilisée par les mâles est reliée à leur niveau d'activité. Nous avons capturé les tamias durant un été avec une saison de reproduction et un été sans. Nous avons quantifié le niveau d'activité par des tests d'arène. Nous avons aussi calculé le domaine vital et la surface explorée par les tamias par la méthode des polygones minimum convexes (PMC). Nos résultats montrent que le domaine vital des mâles variait selon la présence ou non d'une reproduction, tandis que celui des femelles n'était pas affecté par la reproduction. Le niveau d'activité des mâles était relié positivement au domaine vital durant la reproduction, mais négativement en absence de reproduction. Les domaines vitaux diminuaient avec la proportion de mâles aux alentours. La surface explorée par les mâles était affectée par la reproduction, tandis que celle des femelles ne variait pas selon les années. La surface d'exploration des mâles n'était pas affectée par leur niveau d'activité. Nos résultats montrent que les traits de personnalité peuvent être reliés à l'utilisation de l'espace par les mâles durant la reproduction. La surface explorée n'est cependant pas un indice valide de la recherche de partenaires sexuels.

ABSTRACT

In most species, males and females show contrasting reproductive behaviours. While females typically aim at maximizing resources devoted to breeding and male quality, male reproductive tactics aim at maximizing access to females. In some rodent species, male mate searching often takes place before the mating season, as males visit females on their home ranges. Male mate search may be affected by personality traits such as activity/exploration level. In this study, we assess how inter-individual differences in activity and exploration affect male space use, which is likely to reflect the area used for mate searching in an eastern chipmunk population. Our objectives were (1) to compare male and female home ranges over two years with and without reproduction and (2) to determine if the area exceptionally visited by a male during reproduction is related to his activity/exploration level. We live-trapped individuals during a summer when reproduction occurred and a summer when no reproduction occurred. We quantified activity and exploration by using an open-field test. We also computed the home range and the area exceptionally visited using the minimum convex polygon (MCP) methods based on captures. Our results showed that male home ranges varied between the two years, whereas female home ranges did not. Activity/exploration of chipmunks had a positive effect on home range during the year with a summer reproduction, but a negative one when no reproduction occurred. Home ranges decreased with an increasing proportion of surrounding males. AEV decreased for males between the two years whereas it increased for female. The activity/ exploration score did not affect AEV. Our results show that personality traits may be linked to male space use during reproduction in species where mate search is a major determinant of reproductive success. However, AEV is not an informative index of male mate searching.

Keywords: activity, exploration, mate searching, space use, personality, *Tamias striatus*.

2.1 INTRODUCTION

Males and females of most animal species show contrasting reproductive behaviours (Andersson, 1994; Shuster and Wade, 2003). These differences between the sexes stem from the fact that, whereas female reproductive output is mainly limited by gamete production and often by parental care, male reproductive output is mostly limited by access to mates (Trivers 1972). As a result, male mating tactics aim at maximizing copulations and fertilization of potential reproductive partners (Andersson, 1994; Shuster and Wade, 2003). The way males maximize access to females depends on dispersion of receptive females in space and time. For example, if females are spatially clumped, or reproduce asynchronously, males may defend access to a particular female against other males. In such context, traits providing competitive advantages in male-male competition should be correlated to mating success (Clutton-Brock, 1989; Emlem and Oring, 1977). For example, body mass, body condition, or the size of weapons play important roles on mating success in ungulates (Coltman *et al.*, 2002), salmonids (Gross, 1985, 1996), and dung beetles (Moczeck and Emlen, 2000).

If, on the contrary, females are dispersed in space or come in oestrus synchronously, males cannot monopolize their access, and scramble competition is usually observed (Schwagmeyer and Woontner, 1986). In species showing scramble competition, a male has to locate the female and mate with her before his rivals. In such cases, male mobility and traits enabling males to locate females efficiently are more likely to be related to mating success (Andersson, 1994; Schwagmeyer and Woontner, 1986). For example, in the fruit flies (*Drosophilae* sp), scramble competition seems to select for larger males (Partridge, Hoffmann and Jones, 1987). Larger body size in male *Drosophila* confers a mating advantage because larger males run faster, and they are thus able to follow receptive females more efficiently than smaller males (Partridge, Ewing and Chandler, 1987; Partridge and Farquhar, 1983). Scramble competition between males can also favour sensory structures, giving a mating advantage through an increased female detection (Bertin and Cézilly, 2003a, b; see Gwynne and Bailey, 1999 for a study on female sensory structures; Holwell, Barry and

Herberstein, 2007; Obara, 1979). Scramble competition can also favour some cognitive capabilities of males (Andersson, 1994; Spritzer, Solomon and Meikle, 2005). Male mate searching behaviour can also improve females location/detection and thus be related to mating success (Dickinson, 1992; Lane, 2008; Schwagmeyer, 1995; Schwagmeyer and Parker, 1987; Stockley, Searle and Jones, 1994).

In some rodent species, mate searching often takes place just before the mating season, as males visit females on their home ranges prior to oestrus (Elliott, 1978; Schwagmeyer, 1995; Schwagmeyer and Parker, 1987; Stockley, Searle and Jones, 1994). Visits to females are likely to be reflected in the patterns of space use of males, and this explains why the space used by males from polygynous rodent species typically expands during the mating season whereas the space used by females remains constant (Brenner *et al.*, 1978; Spritzer, Solomon and Meikle, 2005; Stockley, Searle and Jones, 1994). The need for reproductive males of such species to leave their territory and search for females may explain why sex-differences in spatial learning abilities are consistently found in polygynous rodent species, whereas they are absent in monogamous rodent species (Gaulin and Fitzgerald, 1986; Gaulin, FitzGerald and Wartell, 1990). Spatial ability and memory thus seem to be favoured in males by sexual selection. In the meadow vole (*Microtus pennsylvanicus*), for example, males that performed better in a water maze test, measuring their spatial abilities, mated with more females in the wild (Spritzer, Solomon and Meikle, 2005). This may suggest that increasing the number of visits per female while visiting as many females as possible may enable a male to assess female reproductive state and gather information on potential mate locations (Luttbeg, 1996; Schwagmeyer and Parker, 1987).

However, most of these studies used a comparative approach, focusing on sex-differences in spatial ability only, in species with monogamous and polygynous mating system. These studies used maze tests conducted in the laboratory, involving mainly spatial learning, but rarely linked individual spatial ability to their behaviour in the wild (but see Spritzer, Solomon and Meikle, 2005). Moreover, individual activity during the maze test is likely to affect spatial learning measurements. Indeed, spatial ability measurement relies on the number of times an individual chooses a wrong path in the maze, and more active individuals

may thus make more "mistakes" because they move more in the maze. Some attempts have been made to dissociate spatial ability measurements from activity (Gaulin, FitzGerald and Wartell, 1990). However, we can expect, based on increasing evidences in many species, that individual males will differ consistently in their level of activity and exploration, which is a personality trait (Gosling, 2001; Réale *et al.*, 2007; Wilson *et al.*, 1994). This expectation arises from the general observation that, even if individuals can adjust their behaviour to a specific environmental condition (Krebs and Davies, 1997), they show consistent behavioural differences across situations and over time (Réale *et al.*, 2007; Sih *et al.*, 2004). For example, even though all individuals can decrease their activity in presence of a predator to reduce their conspicuousness, and increase it when they are foraging (Houston, McNamara and Hutchinson, 1993; Sih, Kats and Maurer, 2000, 2003), some are consistently more active than others (Réale *et al.*, 2007; Sih, Bell and Johnson, 2004; Sih *et al.*, 2004; Sih, Kats and Maurer, 2003). Personality traits also influence some reproductive behaviours such as extra-pair copulation (Van Oers *et al.*, 2008), suggesting that sexual selection may play a role in the evolution of animal personality (Van Oers *et al.*, 2008). Male intrinsic activity and exploration level may have profound effects on mate search, and so greatly affect mating success.

In this study, we used the eastern chipmunk (*Tamias striatus*) as a model species, and trapping data collected over two summers (2006 and 2007) in a marked wild population to assess how activity/exploration level affects male space use. Prior to the mating season, male eastern chipmunks make "inspection bouts" and visit females on their territory, possibly to assess females reproductive state and gather information on their location. A given female chipmunk comes into oestrus for only one day, during which males aggregate on her territory and try actively to copulate with her (Elliott, 1978). Because females come into oestrus relatively synchronously, within four to five weeks (Elliott, 1978; Smith and Smith, 1975), males may face a trade-off between the number of females visited and the time spent with each female. Depending on their activity and exploration level, males could show continuous variation in the number of females visited (and consequently on the supplementary area used for reproduction). Less active/exploratory males should focus their mate search effort on fewer nearby females, whereas more active ones should instead visit more females, located

on a wider area (Stockley, Searle and Jones, 1994). We took advantage of the fact that, in this chipmunk population, reproductive season alternates between spring (March-April) and summer (June-July) depending on the year. Summer space use is thus related to reproductive season and mate searching in years with summer reproductive seasons, but not in years where reproduction occurs during the spring. By comparing male space use during two consecutive summers, we can assess how reproduction (and consequently mate searching) affects space use.

We assessed between-sex differences in activity and exploration level and individual reproduction-oriented space use. We compared space use in males during and outside a reproductive season with that of females during both reproductive and non-reproductive seasons. Only male space use is assumed to increase during reproduction. Furthermore, the availability of females should affect male space use.

Our first objective is to compare male and female summer home ranges (estimated by trapping locations) over a year where reproduction occurred during the summer and a year where it occurred during the spring. We predict that males will use a wider area during the reproductive season, as opposed to the year where no summer reproduction occurred. On the contrary, the area used by females should not differ between the two years. We therefore expect sex-differences in summer space use during the year with summer reproduction only. Our second objective is to determine if the supplementary area used by males during the reproductive season (potentially related to mate searching) is related to his activity/exploration level measured from open-field tests. We expect more active/exploratory males to use a wider area than less active/exploratory ones.

2.2 METHODS

Study site and species

The study site is a 500 x 500 m area of semi-closed deciduous forest dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), which is located near Sutton in southern Quebec, Canada (45°05' N; 72°25' W). Eastern chipmunks are small diurnal and solitary rodents that are active above ground from April to November. They are found in deciduous and relatively mature forests, but some studies report more bushy and open habitat (Elliott, 1978; Snyder, 1982 and references therein). The geographic range of the species extends from Lake Manitoba to the Quebec coastline, northward to the Anticosti island and southward to the Gulf of Mexico (Snyder, 1982). Chipmunks feed on nuts, seeds and acorns, but may also eat tubers and prey on insects (Landry-Cuerrier, 2008; Snyder, 1982). They spend the winter on food reserves hoarded during the summer and show winter torpor (French, 2000; Scott and Fisher, 1972). Females may come into oestrus in early spring (March-April) and in summer (June) (Snyder, 1982; Wrigley, 1969; Yahner, 1978b; Yahner and Svendsen, 1978) but some pregnancies have been reported during the fall (Smith and Smith, 1975). Our study site is located in the northern part of the eastern chipmunk's distribution area, and reproduction alternates between years between spring and summer reproductions. Juvenile emergence suggests that female oestrus periods are relatively synchronized in this species (Elliott, 1978). Individual home ranges reported in the literature vary from 400 to 15 000 m^2, are relatively symmetrical and centered on the burrow (Blair, 1942; Yahner, 1978a; Yerger, 1953).

Live trapping and burrow location

We live-trapped individuals from May to November in 2006 and 2007 using 255 Longworth traps (Longworth Scientific Instruments Ltd, Abingdon, UK) located at 40 m intervals on a flagged grid (the grid is pictured in Figure II-1). Traps were baited with peanut butter and

were usually opened in the morning, checked every 2 hours, and closed around sunset. We marked individuals with two metal ear tags (National Band and Tag Co., New York, KY), one unique Trovan PIT tag (Eidap Inc, Alberta, Canada), and recorded their sex. Prior to reproduction, male testes become scrotal and undergo an important increase in size. The scrotum takes a darker, hairless aspect. Males with testes in scrotal position and a dark scrotum were considered as reproductive. Reproductive and lactating females can be distinguished by their swollen nipples with little/no fur around the nipple. Females that never reproduced can be distinguished by their small nipples hidden in the fur. Individuals were weighted to the nearest gram with a Pesola spring balance (Science Import Inc., Quebec, Canada). Age class (juvenile or adult) was determined according to body weight at first capture and reproductive status. Individuals captured below 70 g and that did not reproduce were considered as juveniles. At every subsequent capture, we recorded date, hour, trap location and body weight, along with the reproductive status of individuals (reproductive vs. non-reproductive males, non-reproductive vs. reproductive or lactating females).

Reproductive events and seasons

We observed a large number of emerging juveniles at the end of the summer 2006 (53 pups were captured between August 29th and October). Furthermore, in June 2006 we observed several mating events and mating chases. In comparison, a massive emergence of juveniles was observed in May-June in 2007 but no new juvenile was captured from August to October 2007. These observations indicate the presence of a mating period in May-June 2006 and one in March-April in 2007, but no mating period in May-June 2007. The 2006 mating period was followed by an abrupt decrease in above-ground activity in August. Chipmunks then began to be active again during the fall, mostly to forage (Landry-Cuerrier, 2008). We thus considered August 1st as the end of the mating period in 2006. We used data on all the captures made between May 1st and August 1st in 2006 and between the same dates in 2007. Summer home range estimates computed in 2006 thus refer to chipmunks in a reproductive season, whereas those computed in 2007 are not related to any reproductive activity.

Open-field tests

We quantified activity and exploration by using an open-field test, where the time spent active/exploratory by an individual in a novel environment is measured (Archer, 1973; see Martin and Réale, 2008 for a detailed description of the test). Briefly, the arena consisted of a rectangular white plastic box (80x40x40 cm) with a Plexiglas lid. Open-field tests were conducted on the grid from May to November in each year to test individuals twice over the two years. Once captured, chipmunks were carried in the trap from their capture location to the open-field arena (distance ranging from 15 to 250 m; mean = 131.8 ± 85.7). Animals were allowed to rest for 3 min in the trap without any movement and were then taken gently out of the trap, transferred into a mesh bag, weighed to the nearest gram and transferred to the entrance of the arena without any direct manipulation. They were pushed into the arena, and their behaviour was recorded for 3 min using a video camera placed on top of the arena. The experimenter remained silent at a distance of 2 m from the open-field apparatus.

Activity/exploration measurements

We kept a minimum of 15 days between tests performed on the same individual. Chipmunk behaviours during the test were scored using the software The Observer (Noldus) and an ethogram derived from Martin and Réale (2008). We computed the number of seconds spent active (see chapter I for the detailed description of recorded behaviours) during the total duration of the test (180 s) as an index of activity/exploration.

Statistics

All statistics were performed with the software R (R Development Core Team, 2005). Individual consistency of behaviour in open-field is reported and discussed in details elsewhere (see Chapter I). We used generalized linear mixed models (GLMM, Pinheiro and Bates, 2000) with a quasi-Poisson distribution using activity/exploration as the dependent

variable. Trial order (first vs. second test, fixed effect), and chipmunk identity (random effect) were included as explanatory variables. We tested if the variance component related to individual identity was significantly different from 0 with a log-likelihood ratio test (1 degree of freedom) between a model with individual identity as a random effect and a model without it (Pinheiro and Bates, 2000). We computed the *Best Linear Unbiased Predictors* (BLUPs) for each individual. BLUPs represent the individual deviation from the common intercept for the variable analysed (in our case activity/exploration) (Pinheiro and Bates, 2000). We used computed BLUPs as the measure of activity/exploration level in all subsequent analyses.

We computed the minimum convex polygon including 95% of the captures (MCP_{95}) and 100% of the captures (MCP_{100}) for the adults using the *adehabitat* package for R (Calenge, 2006; R Development Core Team, 2005). In order to analyse space use by individual chipmunks, we considered MCP_{95} as an index of home range. The MCP_{95} includes most of the space over which a given chipmunk was captured, but excludes some points located farther on the periphery and could thus potentially not reflect inspection bouts made by males during the reproductive season. We thus computed an index of the area exceptionally visited (AEV), as the difference between MCP_{100} and MCP_{95}. More precisely, we analysed MCP_{100} with a linear model while using MCP_{95} as a covariate (i.e. we "corrected" MCP_{100} for MCP_{95}, see below). AEV is supposed to reflect the area located at the periphery of the actual home range, and that is visited on an exceptional basis (for example during mate searching or exploration). We included only the adult chipmunks captured more than 5 times during the field season for a given year, as the package we used could not compute MCP areas from a smaller number of locations. MCP estimations may be biased by the number of locations used to compute the MCP and edge effects (i.e. fewer traps are available to capture individuals at the border of the grid). Thus, the number of locations for each individual was included in every model using MCP as the response variable and we weighted MCP areas by the reciprocal of the distance from the centre of the grid to the individual's location in all models using MCP as the response variable. This enabled us to partly correct for edge effects and maximize available degrees of freedom in our models.

Burrow location was used when available. Burrow location was not available for 16 out of 66 individuals in 2006 and for 27 out of 137 individuals in 2007. For these individuals, we replaced the unknown burrow location by the centre of mass of the MCP_{95} (computed in R, using the adehabitat package Calenge, 2006; R Development Core Team, 2005). The centre of mass of the MCP_{95} may be seen as the estimate of the "mean" location where we may expect to find an individual. To test if the centre of mass was an adequate estimate of burrow location, we performed all the statistical analyses described below using only individuals with a known burrow location. These analyses yielded results similar to those obtained using our full dataset. We estimated local sex-ratio as the proportion of neighbours within 300 m of the burrow of the focal individual (N_n, see above) that were males. Average sex-ratio was 0.43 in 2006 (range: 0.41; 0.48), and 0.41 in 2007 (range: 0.34; 0.49).

To assess whether MCP_{95} is affected by individual characteristics or environmental variables, we fitted a linear model on MCP_{95} as a function of sex, year, activity/exploration score, local sex-ratio, and number of locations used to compute the MCP_{95} as well as their two-way and three-way interactions as explanatory variables. MCP_{95} was log transformed, and all explanatory variables were centered on the mean prior to analysis (Pinheiro and Bates, 2000). The model was simplified in a stepwise manner, by removing all non-significant terms to obtain the selected model. To test whether more active individuals showed larger AEVs, we fitted a linear model on MCP_{100} as a function of MCP_{95} (log transformed; main effect only). We also included sex, year, activity/exploration score, local sex-ratio, number of locations used for MCP estimation as well as their two-way and three-way interactions as explanatory variables. MCP_{100} was log transformed, and all explanatory variables were centered on the mean prior to analysis (except MCP_{95}). Some studies on other sciurids found a relationship between activity and exploration level in the open-field and the frequency of capture (Boon, Réale and Boutin, 2008). If more active individuals were trapped more often, a positive relationship could arise between MCP_{95}, which is supposed to increase with the number of captures, and activity/exploration score. To account for this possible relationship, we computed the correlation coefficient between activity/exploration score and the number of time a given chipmunk was captured each year.

2.3 RESULTS

Areas of capture

Overall, 169 individuals were caught in 2006 (88 were classified as adults, 67 as juveniles and 14 individuals as undetermined age because of lack of information on their reproductive status) and 261 in 2007 (116 adults, 60 juveniles and 85 as undetermined age). MCP_{95} was computed for 42 adults in 2006 (24 females; 18 males) and 94 adults in 2007 (46 females; 48 males). Some examples of MCP_{95} for males and females for both year are presented Fig. II-1. The number of locations used for each individual averaged 12.22 (range: 5; 44). The mean MCP_{95} for males and females both years are presented in Fig. II-2. In 2006, the average MCP_{95} were respectively 6444 m^2 (range: 0; 13600) for males, and 2258 m^2 (range: 0; 10400) for females. In 2007, MCP_{95} were 1754 m^2 (range: 0; 10000) for males and 1048 m^2 (range: 0; 8400) for females.

Sex of chipmunks had a significant effect on MCP_{95}. Overall, males had significantly bigger MCP_{95} than females. However, the non-significant year effect and the significant negative interaction between sex and year suggest that male MCP_{95} differed between the two years, whereas female MCP_{95} did not change significantly (Table II-1 and Fig. II-3). An interaction between year and activity suggests that activity/exploration score had no significant effect on MCP_{95} in 2006, whereas it had a negative one in 2007 (Table II-1and Fig II-4). The proportion of males around an individual's burrow had a negative effect on MCP_{95}, meaning that chipmunks tended to decrease their MCP_{95} when surrounded by more males (Table II-1). MCP_{95} of both sexes increased with the number of captures. All rejected interactions had $p > 0.3$.

Activity/exploration level was not related to the number of times a chipmunk was captured in any year (2006: cor = -0.092; p = 0.496; 2007: cor = -0.197; p = 0.184; see Fig.II-5).

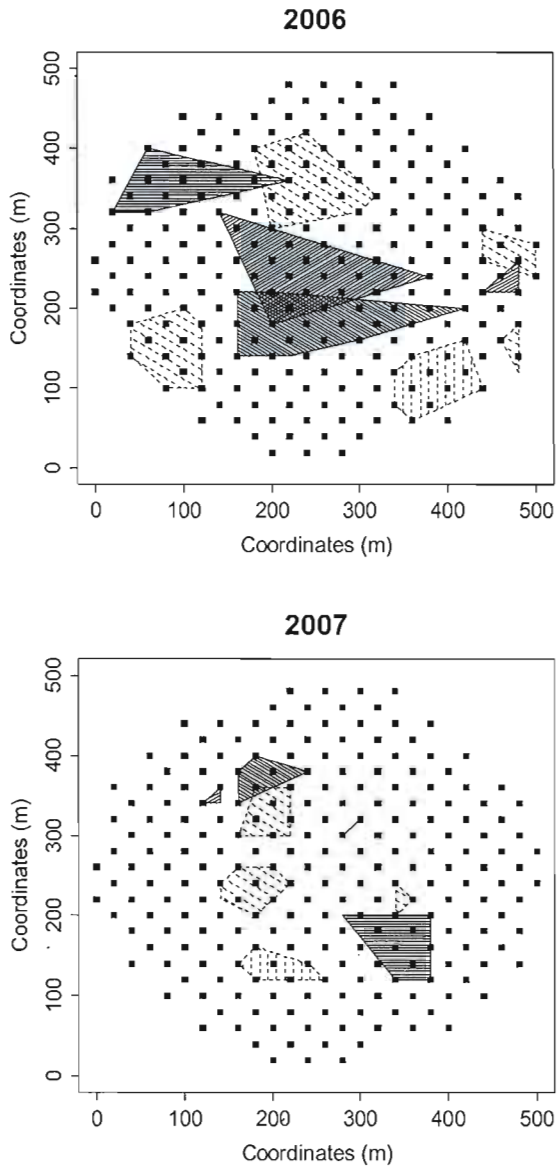

Figure II-1 Examples of MCP_{95} computed for adult males and females chipmunks in 2006 and 2007. Male MCP_{95} (solid lines) and female MCP_{95} (dashed lines) were chosen to represent the variability of individual MCP_{95} within each year.

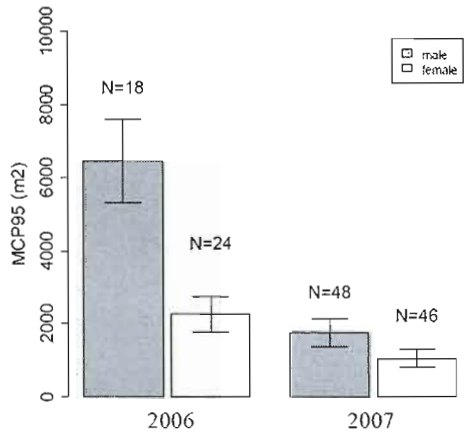

Figure II-2 Mean MCP_{95} (± s.d. of the mean) of summer trapping locations for individuals according to their sex, in 2006 (breeding season) and 2007 (no breeding season).

Table II-1 Final model for the MCP_{95} of chipmunks in 2006 and 2007.

MCP_{95} (log transformed)			
Factor	**Coefficient ± s.e.**	**T**	**Df**	**P**
Intercept	4.57 ± 0.78	5.87	1, 52	**< 0.001**
Number of locations	0.17 ± 0.04	3.99	1, 52	**< 0.001**
Sex[†]	2.82 ± 0.96	2.96	1, 52	**0.004**
Year[‡]	1.50 ± 1.19	1.27	1, 52	0.211
Sex-ratio	-28.38 ± 11.63	-2.44	1, 52	**0.018**
Activity	0.72 ± 0.51	1.40	1, 52	0.166
Sex X year	-4.67 ± 1.23	-3.79	1, 52	**< 0.001**
Year X activity	-2.27 ± 0.93	-2.45	1, 52	**0.017**

Adjusted $R^2 = 0.56$; $F_{7, 52} = 11.7$; $p < 0.0001$.

[†]female is the reference.

[‡]2006 is the reference.

Variables initially included in the model were number of locations, activity/exploration score, sex-ratio, year, sex and all their two-way and three-way interactions.

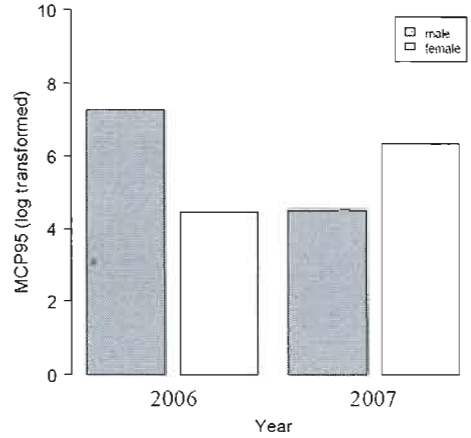

Figure II-3 Predicted MCP_{95} (log transformed) for male and female chipmunks in 2006 (breeding season), and 2007 (no breeding season).

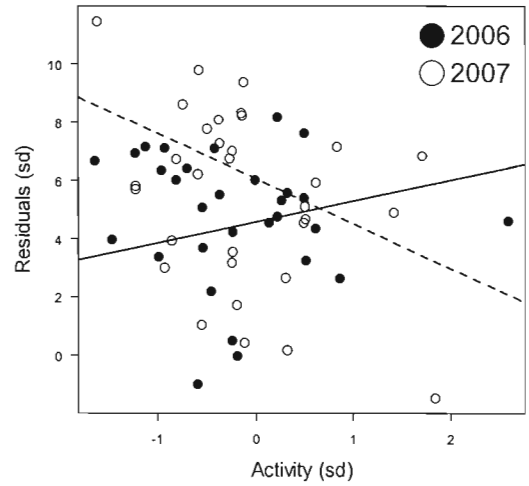

Figure II-4 Residuals of MCP_{95} (log transformed) as a function of activity. Residuals were obtained by predicting the effect of each term in the model (except the interaction year x activity; Table II-1) and substracting the predicted values from the observed MCP_{95} value of each individual. Activity slope is different between 2006 (solid line) and 2007 (dashed line).

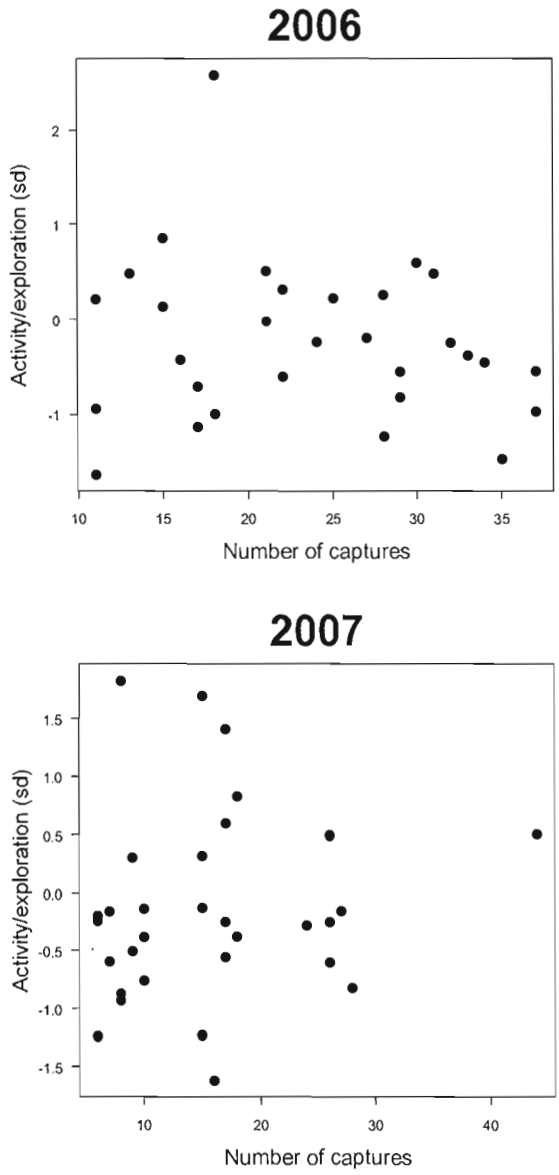

Figure II-5 Relationship between activity/exploration level measured in open-field tests and number of captures for eastern chipmunks in 2006 and 2007.

AEV area

MCP_{100} was strongly related to MCP_{95} (see Table II-2). Overall, chipmunk AEV (MCP_{100} "corrected" for MCP_{95}) was not affected by sex or year, but the interaction between sex and year suggested that AEV decreased between 2006 and 2007 for males, whereas it increased during the same time period for females (Table II-2 and Fig. II-6). All other variables and their interactions were rejected from the model with $p > 0.2$.

Table II-2 Final model for the area exceptionally visited for chipmunks in 2006 and 2007 (obtained by analyzing MCP_{100} while including MCP_{95} as a covariate). MCP_{100} and MCP_{95} were log transformed.

AEV (log transformed)				
Factor	**Coefficient ± s.e.**	**T**	**Df**	**P**
Intercept	3.27 ± 0.67	4.86	1, 55	**< 0.001**
MCP_{95}	0.59 ± 0.08	7.04	1, 55	**< 0.001**
Sex[†]	0.95 ± 0.59	1.60	1, 55	0.114
Year[‡]	0.72 ± 0.59	1.21	1, 55	0.230
Sex X year	-2.04 ± 0.93	-2.17	1, 55	**0.034**

Adjusted $R^2 = 0.65$; $F_{4, 55} = 29.01$; $p < 0.0001$.

[†]Female is the reference.

[‡]2006 is the reference.

Variables initially included in the model were activity/exploration score, sex-ratio, year, sex, number of locations, and all their two-way and three-way interactions, as well as MCP_{95} (main effect only).

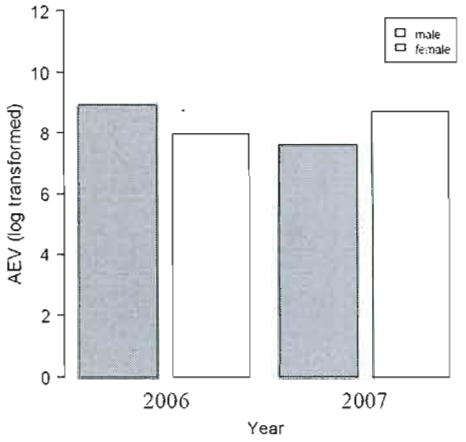

Figure II-6 Interaction between sex and year for chipmunk AEV in 2006 and 2007. AEV decreased between 2006 and 2007 for male chipmunks whereas it increased for females.

2.4 DISCUSSION

Our objectives were first to compare male and female home ranges during and outside the summer reproductive season. Males had a much larger home range (MCP_{95}) in 2006 than in 2007, whereas female MCP_{95} did not differ significantly between years. Furthermore, home range was not affected significantly by activity/exploration level in 2006, but MCP_{95} decreased with activity/exploration score in 2007. An individual's home range decreased with an increasing proportion of surrounding males. AEV was not related to individual activity/exploration level measured in an open-field, or sex ratio. AEV of males decreased between 2006 and 2007, whereas AEV of females increased between the two years.

The bigger MCP area for males in 2006 as well as the difference between the MCP_{95} of males between the two years indicates that male chipmunks use a supplementary area during reproduction. Males had a mean capture area (MCP_{95}) of 6444 m^2 whereas females averaged 2258 m^2, which yields a ratio between male and female space use of 2.85 during the reproduction. Sex differences in space use are frequently reported in this species, but tend to be smaller, most likely because MCP area is seldom measured with an explicit reference to the reproductive state of the individuals. For example, Yerger (1953) reported minimum polygons using summer trapping data over two years averaging 1500 m^2 for males (range: 566; 2670) and 1052 m^2 (range: 404; 2468) for females, yielding a ratio of 1.4. Yerger's study reports the presence of juveniles on the study site, and space use by adults should thus be related to at least one reproduction over the two years. On the contrary, Blair (1942) reported no sex differences, with space use averaging 9305 m^2 for males and 8700 m^2 for females (ratio of 1.06). This study used trapping data collected only on a small time period during the fall, and is therefore less likely to be related to any reproductive event. According to Elliott (1978) male eastern chipmunks venture out of their territory to make "inspection bouts" prior to mating with females. Inspection bouts should translate into bigger capture areas. Most studies on chipmunk space use used MCP_{95} as a classical measure of home range. We argue that MCP_{95} computed in this study during the summer reproduction reflects, in part, the mate search behaviour expressed by males just prior to the mating season. Similar

patterns have been reported in a few other sciurids with a similar mating system involving scramble competition. For example, the area used by a given male red squirrel during reproduction is related to the number of mating chases he attends and to his reproductive success (Lane, 2008). Likewise, Koprowski (1993) describes mating chases involving males that were as far as 600 m from their own territories.

Male with bigger MCP areas may have been able to encounter or visit more receptive females. Visits to females may enhance how a male can accurately estimate the timing of a female's oestrus, as well as provide him with information about her space-use patterns (Luttbeg, 1996). Visiting the female's territory prior to the oestrus day has also been hypothesized to give a competitive advantage in direct competition between males on the day of oestrus, because the male that visited the female more often before her oestrus has a better knowledge of her territory and thus a competitive advantage during agonistic interactions (Stockley, Searle and Jones, 1994). According to Elliott (1978), agonistic interactions between two adult chipmunks seem to be won by the chipmunk who is closer from its own burrow. This may suggest that the knowledge or familiarity of the habitat may confer a competitive advantage during agonistic interactions in this species. This last hypothesis (i.e. that familiarity with the female's territory may give an advantage) would thus be particularly relevant in the eastern chipmunk mating system.

Space use estimations using trapping data and minimum polygon calculations reported in the literature range between 768 and 12542 m^2 for eastern chipmunks (Elliott, 1978; Yahner, 1978a and references therein). This range is rather large, which suggests that the space used by individuals is influenced by many factors. The home range of an individual is the spatial expression of the behaviours that this animal performs in order to survive and reproduce (Börger *et al.*, 2006; Burt, 1943). Apart from reflecting mate searching behaviours, home range is primarily thought to reflect the amount of resources needed by individuals to meet their energy requirements. Optimal models consider that the amount of resources in each individual home range should be roughly the same (optimality models of resource-based space use are reviewed in Adams, 2001). Consequently variation in individual home ranges should be related, at least in part, to variation in resources included in home ranges. This is

supported by the negative relationship between space used by individuals and resource density frequently found in the wild (Gass, Angehr and Centa, 1976; Turpie, 1995). However, in these studies, population density generally increases with resource abundance, and it is possible that resource abundance may result in smaller home ranges because of an increased population density. In our study, food abundance varied between years because of a massive release of seeds by masting trees during the fall 2006. It is possible that a portion of the seeds hoarded by chipmunks in 2006 was still available in their burrow during 2007. In this case, resources would have been more abundant in 2007 compared to 2006 and this may partly explain the smaller MCP_{95} areas found in 2007 compared to 2006 for both sexes. Furthermore, chipmunk density increased in 2007, because of the massive emergence of juveniles on our study site at the beginning of the summer that year. However, even if resource abundance or chipmunk density may explain the difference in mean space use between years, it cannot account for the large sex-differences in space use we found during the reproductive period of 2006. It is also important to note that the classic optimality view presented above (predicting a negative relationship between space use and resource abundance) does not seem to hold completely for the eastern chipmunk. Indeed, some studies have found a positive relationship between chipmunk home range areas and the basal area of mast-producing trees (an index of seed production in the area, Lacher and Mares, 1996; Mares and Lacher, 1987). Such studies suggest that resource density (and its effect on population density) cannot account alone for the important variation in home range size reported for the eastern chipmunk in previous studies, as well as between individuals in this population.

We also found that activity/exploration level of chipmunks affected MCP_{95} differently between the two years. This interaction suggests that activity/exploration level of chipmunks may interact with environmental conditions and thus that its potential effect on aspects of individual's ecology such as space use may be difficult to detect and unravel. Our study suffers from a relatively limited sample size, and understanding how activity affects MCP_{95} would require more data.

The proportion of males surrounding the burrow of a given chipmunk was negatively related to its MCP_{95}. This relationship seemed to hold for both sexes and on both years, suggesting that home range may be limited by aggressive encounters. Chipmunks typically show important home range overlap (Elliott, 1978; Getty, 1981), and aggressive behaviours (mostly chases) are typically reported has the most frequent social interactions between adults (Elliott, 1978). Precise analysis of the aggressive interactions in the wild suggests that the chances a chipmunk has to win an encounter decreases with the distance from his burrow (Dunford, 1970; Elliott, 1978). Moreover, studies conducted in captivity report quite high aggression levels between chipmunks, with some intensive fights leading to death. In such studies, males are typically dominant over females, a trend seemingly related to body mass (Ickes, 1974 in Elliott, 1978; Wolfe, 1966). Thus, in our study, chipmunks surrounded by a greater proportion of males, may face more aggressive interactions, or incur more costs from such interactions.

Many studies used mean MCP area as a measure of home range. However, the large range of MCP areas we found between individuals within each sex in this study strongly suggests that this measure of space use should instead be taken as a relative index of home range size. Indeed, we captured some individuals systematically at one location, yielding a null MCP_{95}, whereas some were captured over half of our trapping grid. Home range estimations based on minimum polygons may be biased for individuals that were captured less often. Moreover, individuals could differ in their willingness to enter into traps, for example because they differ in personality. Boon, Boutin and Réale (2008) show that female red squirrels with a high activity level in the open-field were more likely to enter traps. Thus, differences in capture frequency between individuals could yield individual differences in MCP area just because more locations are available for active individuals. As a result, a positive relationship could arise between activity/exploration level and MCP area. This bias is however unlikely in this study system, as we found no relationship between activity/exploration level of a given chipmunk and the number of times this chipmunk was captured. Furthermore, we took the number of captures into account in all our models.

Although some of the between-male variation in MCP_{95} is likely to be related to unmeasured factors and to our calculation methods, important differences in space use during reproduction suggests that males may adopt alternative tactics in order to reproduce. Differences in mate search behaviour have commonly been related to alternative male mating tactics in various species with a scramble promiscuity mating system (e.g. Farentinos, 1972; Stockley, Searle and Jones, 1994). Alternative mating tactics described until now in sciurid species suggest that, while the global mating system is commonly described as a form of scramble promiscuity, some individuals may choose a tactic based on mate guarding as a mean of maximizing mating success, thereby limiting mate searching effort. For example, in the Grey squirrel (*Sciurus carolinensis*), the most aggressive males guard the receptive female and exclude other males (Koprowski, 1993). When a female succeeds in escaping an aggressive male, a scramble ensues and satellite/non-aggressive males, waiting at the periphery of the female's territory, will try to locate and mate with her. A similar pattern has been reported in the yellow pine chipmunk (*Tamias amoenus*) for which aggressive males guard actively receptive females against other males (Schulte-Hostedde and Millar, 2002b). The study was conducted in captivity and the authors suggested that less aggressive individuals may compensate their low aggressiveness in the wild by being more efficient at locating females (Schulte-Hostedde and Millar, 2002a).

We also produced a relative index of the supplementary area used by males during the reproduction (the area exceptionally visited) and linked it to individual activity and exploration level. Some studies already focused on the link between scramble competition and male spatial ability (see introduction). However, most studies worked on between-sex differences, in order to explain the adaptive nature of the sexual dimorphism found in spatial ability and memory (but see Spritzer, Solomon and Meikle, 2005). Activity level of individuals is sometimes included in such studies as a potential bias (i.e. they "correct" for individual differences in activity while studying spatial ability). Our study thus offers a relatively new perspective, as we aimed at linking individual differences in space use (reflecting mate searching behaviour) and activity *per se* in a species with a scramble promiscuity mating system.

We found that the male AEV decreased when no reproduction occurred, but that the AEV of females increased in the year without reproduction. This interaction is only weakly significant, and should be treated with caution. However, this interaction suggests that male and female AEV may have different functions. For males, a smaller AEV during the year without reproduction compared to the year with reproduction is likely to be related to male mate searching. The fact that females increased their AEV during the year without reproduction could also be related to their reproductive status. In rodents, females may decrease their above-ground activity pattern during gestation and lactation (e.g. Weinandy and Gattermann, 1995 and personal observations on our study site). This decrease in above-ground activity may be due to the necessity of feeding regularly the pups, but lactating females also face important energy needs (Kunkele and Kenagy, 1997; Millar, 1978, 1979) and could reduce their energy expenditure by decreasing their general locomotor activity.

Our index of AEV may not be the most informative way of quantifying the spatial expression of mate searching behaviour. In this study, we chose to use the two MCP areas that are the most widely used in studies of space use and home range. MCP_{100} and MCP_{95} are likely to reflect the same quantities, and a large number of studies using the MCP calculation methods to study home range used MCP_{95} and MCP_{100} as synonyms in small mammals (Blair, 1942; Farentinos, 1972; Halloran and Bekoff, 2000; Yerger, 1953). MCP_{95} and MCP_{100} should thus be affected by the same factors. If this is true, we cannot expect AEV to be an informative index of space used on an exceptional basis, as, by correcting MCP_{100} for MCP_{95}, we may remove the effects of most factors affecting space use. Thus, the absence of any effect by the factors we tested in this study has to be treated with caution, and does not mean that these factors do not affect chipmunk space use.

In conclusion, our study provides evidence that male chipmunks use a supplementary area during the reproduction. Space used was bigger for males during the reproduction compared to the year where no reproduction occurred, whereas female's space used did not differ between years. This supplementary area for males is likely to be related to mate searching behaviour, which is thought to provide an advantage during the oestrus period of females. The area used by chipmunks seemed to be affected differently by activity/exploration level

according to year and to be limited by the proportion of surrounding males. On the contrary, AEV did not prove to be an informative index of male mate searching. AEV of males was smaller in the year with no reproduction compared to the year where a reproduction occurred, whereas we observed the contrary for the AEV of females. This suggests that females decreased their above-ground activity during reproduction, because of the costs and constraints of gestation and lactation. Our study thus shows that personality traits such as activity and exploration may affect space use of individuals in the wild. The effect of activity/exploration level, however, is hard to precise in this study, and should be demonstrated more convincingly with larger sample sizes and data collected over more than two years. Larger sample sizes may also enable us to use more robust and powerful methods than minimum convex polygon calculation.

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CONCLUSION GÉNÉRALE

Le premier objectif de ce mémoire était de préciser la nature des différences de personnalité mesurées dans l'arène par l'utilisation d'une nouvelle méthode d'analyse permettant de prendre en compte le patron temporel d'activité et d'exploration des individus. Cette méthode nous a permis de contourner les biais résultant de différences de patron temporel entre les individus. Notre deuxième objectif était de déterminer si l'activité et l'exploration influencent l'utilisation de l'espace par les mâles durant la reproduction, reflétant le comportement de recherche des partenaires sexuels chez les tamias rayés.

Les individus soumis à un test d'arène répété ont montré un comportement constant et reproductible. Ceci supporte l'idée que le test d'arène fait ressortir les différences comportementales des individus en les soumettant à un stress (Martin et Réale, 2008; Réale *et al.*, 2007). De plus, le niveau d'activité et d'exploration global des individus a diminué entre le premier et le deuxième test. Avec les répétitions, on suppose que le caractère nouveau de l'arène diminue, ce qui entraîne une diminution de l'activité et de l'exploration. Une diminution semblable entre les tests d'arène successifs est rapportée par des études réalisées sur d'autres populations de sciuridés et utilisant un test similaire (Boon, Réale et Boutin, 2007; Martin et Réale, 2007).

Les individus ont également montré des différences constantes au niveau de leur patron temporel d'activité et d'exploration. Ces différences suggèrent que les individus varient au niveau de leur manière de répondre au stress et que certains individus sont plus proactifs que d'autres (Koolhaas *et al.*, 1999). Les individus plus proactifs ont montré un niveau d'activité et d'exploration plus élevé au début du test et une diminution plus importante de leur activité au cours du temps. Les individus à l'opposé du continuum ont montré une réponse caractérisée par un niveau d'activité modéré au début du test mais une plus grande stabilité au cours du temps. Ces réponses pourraient être associées à des patron d'exploration différents :

plus un individu serait proactif, plus il exprimerait un patron d'exploration rapide et superficiel. Le comportement dans un environnement nouveau nous permet donc, non seulement de quantifier la personnalité des individus (c'est-à-dire leur niveau intrinsèque d'activité et d'exploration), mais aussi d'apporter des informations sur leur manière générale de répondre à un stress (Both *et al.*, 2005). En effet, les différences de proactivité suggérées par nos résultats pourraient être reliées à d'autres différences, notamment au niveau de la réactivité des systèmes nerveux sympathiques et parasympathiques, sérotoninergiques et dopaminergiques (Koolhaas *et al.*, 1999).

Puisque le patron temporel d'activité et d'exploration dans l'arène est différent d'un individu à l'autre, la durée du test pourrait affecter la relation entre le score global d'activité et d'exploration, et le niveau de proactivité des individus. Un test court, comme dans notre étude, mène à une relation positive entre le niveau d'activité et d'exploration mesurée dans l'arène et le niveau de proactivité des individus. À l'inverse un test plus long aurait pu mener à une relation négative. Étant donné la grande variabilité de la durée des tests d'arènes rapportés dans la littérature, nous encourageons les études futures à prendre en compte le patron temporel d'activité et d'exploration des individus, de manière à faciliter l'interprétation des résultats. Malheureusement, notre étude ne permet pas de valider nos mesures comportementales par des indices physiologiques comme la réponse hormonale des individus ou le rythme cardiaque. Des études supplémentaires, visant à relier le patron temporel d'activité et d'exploration des individus à des mesures physiologiques seraient donc une prochaine étape à envisager. Nos tests ont été réalisés directement sur le terrain. Certaines mesures physiologiques peuvent être relativement difficiles à prendre en milieu naturel et peuvent impliquer des manipulations plutôt intrusives pour les individus (par exemple, l'étude de la réponse hormonale des individus requiert des prises de sang répétées). Nous pensons cependant qu'il est possible de mettre au point des mesures physiologiques faciles à effectuer et peu envahissantes pour les individus, comme par exemple la mesure du rythme cardiaque, ou respiratoire.

Nous avons également analysé la relation entre le niveau d'activité et d'exploration des individus et leur patron d'utilisation de l'espace durant la reproduction. Pour ce faire, nous

avons calculé deux indices d'utilisation de l'espace. Le domaine vital des individus a été estimé par le polygone minimum convexe comprenant 95% (MCP_{95}) des captures. Nous avons également calculé un indice de la surface visitée sur une base exceptionnelle par les individus. Les mâles ont utilisé un domaine vital presque trois fois plus important que les femelles pendant la saison de reproduction. Les mâles ont montré des différences importantes entre les deux années tandis que les femelles n'ont pas montré de différences. Ce résultat suggère que, les mâles visitant les femelles pour se reproduire, la mesure traditionnelle du domaine vital des individus qu'est le MCP_{95} reflète non seulement les besoins en ressources des individus mais également leur comportement de reproduction. La surface utilisée par les tamias mâles et femelles est limitée par la proportion de tamias mâles autour du terrier, possiblement à cause des interactions agressives entre les adultes, qui devraient être plus dures à gagner et plus risquées lorsqu'elles impliquent des mâles. L'aire utilisée exceptionnellement par les mâles a diminué en absence de reproduction, vraisemblablement parce que cette surface est reliée au comportement de recherche de partenaires sexuels. À l'inverse, cette surface a augmenté en absence de reproduction chez les femelles, suggérant que les femelles diminuent la surface qu'elle utilisent durant la gestation et la lactation. Quelques études ont déjà étudié l'utilisation de l'espace par les mâles dans des systèmes de reproduction polygynes similaires à celui du tamia rayé. Cependant, aucune étude n'a cherché à déterminer si la personnalité des individus influence leur comportement de recherche des partenaires sexuels. Notre étude suggère que la personnalité peut jouer un rôle dans l'utilisation de l'espace des individus, mais des études supplémentaires, sur des échantillons plus importants, et libérées des limitations reliées à la méthode des polygones minimum convexes, sont nécessaires. La localisation des individus par télémétrie, plutôt que par capture serait souhaitable pour les études futures, puisqu'elle permettrait de contourner le biais des MCP pour les individus capturés moins souvent, et de collecter plus de localisations par individu. Il serait ainsi possible d'obtenir des informations plus précises sur l'utilisation de l'espace par les mâles. Des méthodes plus modernes et précises pourraient ainsi être utilisées, comme la méthode des *kernels* (Seaman, Griffith et Powell, 1998; Seaman et Powell, 1996), pour nous permettre non seulement d'estimer l'espace couvert par les mâles, mais également l'intensité de l'utilisation de cet espace. Associées à des observations directes des accouplements, cette méthode nous permettrait également de passer d'un indice relatif de

l'étendue couverte par les mâles, à une mesure plus robuste et validée des visites faites par les mâles aux femelles. Enfin, nous ne possédons pas encore de données sur le succès de fécondation des mâles. Il serait donc souhaitable de faire des analyses moléculaires, nous permettant d'étudier directement le succès de fécondation des mâles et de mieux comprendre comment les différences que nous observons entre les mâles durant la reproduction influencent le succès reproducteur des individus.

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